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## PHOTOGRAPHS AND DESCRIPTIONS OF CUP-FUNGI—XV

### THE GIANT ELVELA<sup>1</sup>

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(WITH PLATE 29)

In April, 1931, the writer received from Dr. Leva B. Walker, of the University of Nebraska, an unusual specimen of *Elvela* collected by Dr. W. E. Bruner of Baldwin, Kansas. As pointed out by Dr. Walker, this specimen is like the illustration in Hard's mushroom book under the name of *Gyromitra esculenta*. His species, however, was wrongly named and the illustration (figure 418) was referred by the writer in North American Cup-fungi to *Elvela caroliniana* of which the European form *Elvela Gigas* Krombholz was cited as a synonym.

There is a great deal of speculation as to what the Krombholz plant really was. The specific name *Gigas* indicates that it was a giant form. In the description it is stated that it was 4 to 12 inches high and broad. The spores are described as large and ellipsoid. The term large here is doubtless used in contrast with those of *Elvela esculenta*, which was listed in the same work and in which the spores are very much smaller. From the colored illustration accompanying his work the pileus is noted to be chestnut-brown.

Boudier's illustration of the Krombholz species shows the spores to be more fusoid than those of our specimens. Also,

<sup>1</sup> This paper is supplementary to The North American Cup-fungi (Operculates), which was published by the author and issued December, 1928.

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the convolutions of the pileus seem to be less intricate. Our plant agrees fairly well with Krombholz's description and for the time being it is referred to that species. For a complete synonymy and description see North American Cup-fungi (Operculates), page 253. The specimen shown in accompanying illustration was eight inches high. The pileus was five inches broad and chestnut-brown. The stem was three and one-half inches at the base and two and one-half inches at the narrowest point. The spores are ellipsoid, and contain one large oil-drop with usually several smaller ones and at maturity are rough and  $12-14 \times 30-36 \mu$ . On close inspection they are found to be delicately reticulated. In a later letter we learned that one of the specimens collected by Dr. Bruner was ten and one-half inches high, the largest record received to date.

The writer would be glad to receive any specimens or photographs of this and related forms looking toward a revision and extension of our knowledge of the Elvelaceae. The species of this family are so variable in form that photographic records should accompany specimens whenever it is possible to get them.

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# STUDIES ON THE MORPHOLOGY AND DEVELOPMENT OF AN INSECT-DESTROYING FUNGUS, ENTOMOPHTHORA SPHAEROSPERMA<sup>1</sup>

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(WITH PLATES 30 AND 31 AND 1 TEXT FIGURE)

## INTRODUCTION

Few entomogenous fungi have received more attention, either from mycologists or from entomologists, than *Entomophthora sphaerosperma*; nevertheless, the supposedly obligate parasitism of this species has presented difficulty to its complete study. The writer's success in cultivating the fungus on artificial media has made possible the detailed observation of all phases in its life cycle, and the results are presented in this paper.

## TAXONOMIC HISTORY

*Entomophthora sphaerosperma* was named by Fresenius (6) in 1856, and in 1858 he published a brief description (7), based mainly upon the size and appearance of the resting spores. It is probable that Fresenius did not observe the conidial stage, for although he mentioned another type of spore, his figures indicate that these spores and the mycelium which bore them belonged to some Hyphomycete. The host upon which Fresenius found the fungus was the "cabbage worm," the larval stage of *Pieris Brassicae*.

Brefeld, in a series of papers (2), (3), (4) from 1870 to 1881, described a fungus, also parasitic upon larvae of *Pieris Brassicae*, which he first (1870) called *Empusa radicans*, and later (1881) named *Entomophthora radicans*, because of its branched conidiophores.

Cohn (5) in 1870 created the genus *Tarichium*, based upon the

<sup>1</sup> Contribution from the Laboratories of Cryptogamic Botany, Harvard University, No. 104.

characteristics of the resting spores, and he changed Fresenius' name *Entomophthora sphaerosperma* to *Tarichium sphaerospermum*. Cohn, moreover, pointed out that Fresenius' *Entomophthora sphaerosperma* and Brefeld's *Empusa radicans* occurred upon the same host and usually at the same time of year, in late summer. He did not say, however, that the species of Fresenius and of Brefeld were identical. It remained for Sorokin (14) in 1883 to state this point clearly; Nowakowski (10) seems to have failed to note the identity of the two species, for he described the fungus under Brefeld's name of *Entomophthora radicans*. The fungus was first recorded in this country on the clover weevil, *Hypera punctata* (*Phytonomus punctatus*) by Arthur (1), who called it *Entomophthora Phytonomi*; Thaxter (16) subsequently showed that this parasite was identical with *Entomophthora sphaerosperma*. The fungus has since been observed on a wide variety of insects, but because of the early work of Fresenius and Brefeld, the larva of *Pieris Brassicae* is still the most generally known host, especially in Europe.

The writer first observed the fungus in 1923 upon larvae of *Rhopobota vacciniana* Packard, the "black-headed fireworm" that attacks cranberry foliage and fruit; this insect is general in its distribution in both Europe and America, wherever cranberries (*Vaccinium macrocarpon*) occur, but has never previously been reported as a host of this *Entomophthora*. It was from the larvae of this insect that the fungus now in culture was obtained in 1927.

#### TECHNIQUE

A description of the methods employed for growing certain entomogenous species of the Entomophthoraceae in artificial culture has already been given by the writer in an earlier paper (13) and this discussion will be limited to a brief review.

*Entomophthora sphaerosperma* was first grown on flesh of the common herring or alewife (*Pomolobus pseudoharengus* Wilson) after attempts to cultivate the fungus on nutrient agar and other standard media had failed. The herring was autoclaved, and then inoculated with fresh conidia that had been collected on a sterile glass plate, inverted over an infected larva in a moist chamber; these conidia germinated readily, and gave rise to a

pure culture of the fungus. Cultures have also been made by transferring bits of the fungus from an infected insect directly to the culture medium; but despite the utmost precaution, such cultures are always contaminated with bacteria, and a laborious series of transfers is necessary before a pure culture can be obtained.

Subsequently the fungus has been grown on about forty different media, of which swordfish (*Xiphias gladius* Linnaeus) and potato have proved to be the two most useful. Preparation is simple; the substance to be used is cut to fit the tube or flask, sterilized for fifteen minutes at ten pounds' pressure, and inoculated. Potato and swordfish need no adjustment for acidity, for their H-ion concentration is within the range most favorable for growth (pH 6.4 to pH 6.8).

*Entomophthora sphaerosperma* grows best at temperatures of 18° C. to 21° C., but will grow well, though more slowly, at lower temperatures. Stock cultures can be kept in the ice-box for at least two months without transfer, and freezing will not injure the fungus; indeed, it stimulates the germination of hyphal bodies. At ordinary temperatures the fungus does not form resting spores on most media; however, resting spores may be readily obtained in great numbers on autoclaved egg yolk.

The material for the following study was obtained from pure cultures. Careful comparison at different stages has shown the fungus to be identical with corresponding stages of *Entomophthora sphaerosperma* on its insect host.

#### MORPHOLOGY AND DEVELOPMENT

The stages in the life-cycle of *Entomophthora sphaerosperma* will be discussed in the order of their developmental sequence.

1. *Conidia.* The conidia are narrowly elliptical, with rounded apex and a tapering base, which is encircled by a barely perceptible collar, marking the ring of attachment to the conidio-phore (PLATE 30, FIGS. 4-11). Average measurements, which are identical for spores produced on the natural host and upon artificial media, are 22  $\mu$  by 7  $\mu$ . A one-layered membrane, thinnest over the basal portion, encloses the spore. The apex is often crowned by a transparent gelatinous cap, which is more

readily apparent after immersion in weak potassium hydroxide solution, followed by staining (PLATE 30, FIGS. 9-11). This cap, though closely adherent, is not an integral portion of the spore membrane, for it can be displaced by rough handling (PLATE 30, FIG. 10), and its staining reaction is sharply differentiated from that of the underlying conidial membrane. Such a modification of the conidial wall has rarely been observed among members of the Entomophthoraceæ, although it has long been recognized that certain species (*Empusa Muscae* for example) have protoplasm adherent to the exterior of the spore, due to the ejection of the contents of the conidiophore when the spore is shot off. Doubtless both types of material, though of very different origin, aid the spore in adhering to the host. When a conidium is hurled from its conidiophore, its flight is too swift to be accurately observed; but if one collects discharging conidia of *Entomophthora sphaerosperma* on a cover glass placed obliquely to the line of projection, most of the spores will be found with their apices pointed in the direction of flight (the force of impact causes some to spin around on the smooth surface); from this fact it seems reasonable to assume that they do not turn over in the air, but, arrow-like, travel with the apex ahead, in which case the adhesive apical cap is most advantageously placed to anchor the spore when it strikes the host or some other solid object. It is interesting to note that the conidia of an unnamed *Empusa* which the writer has in culture are of the approximately spherical shape characteristic of spores of *Empusa Muscae*, and are also very adhesive, but like the conidia of *Entomophthora sphaerosperma*, no protoplasm adheres to their exterior nor do they possess the gelatinous cap so evident on the spores of the latter species. It will be interesting to learn, when further study has disclosed the condition in other species, whether this structure has any taxonomic significance, as indeed may be the case if its occurrence is restricted to conidia of species with branched conidiophores and elliptical spores.

The protoplasm is evenly and finely granular, and non-vacuolate in newly formed spores; vacuoles begin to form, however, as soon as the spores have access to abundant moisture. A single nucleus, circular or oval in outline, 3 to 4  $\mu$  in diameter,

and centrally located, is always present. Its outline may occasionally be seen in fresh conidia, but details of structure are not visible until the nucleus is stained.

*A. FORMATION AND DISCHARGE.* The process of conidial formation and projection in the Entomophthoraceae is of great interest. The following description is based upon studies of small portions of a culture on potato, which were transferred to a cover glass, and the latter then inverted and sealed over a Ward cell. A very small drop of water was sealed in the tip of each arm of the cell; this method obviated the formation of a moisture film on the cover glass, a difficulty encountered with Van Tieghem cells. When the atmospheric humidity in the glass chamber attained equilibrium, the fungus continued to form conidia under what may reasonably be supposed were favorable and practically normal conditions. Observations were made and drawings outlined with a camera lucida at a magnification of seven hundred and twenty diameters.

Mature conidiophores are digitately branched at the distal end. These tips, to a greater extent than the rest of the conidiophore, are distended with dense, finely granular protoplasm, in which are occasional small vacuoles (PLATE 30, FIGS. 2, 3); numerous nuclei also occur, either linearly arranged or obliquely placed in pairs. Each branch is partitioned by one or more cross walls, most frequently by a single septum near the tip, and the terminal portion thus cut off is usually, but not always, uninucleate.

The conidium first appears as a small translucent bud upon the blunt end of a branch; protoplasm flows in from the conidiophore, and ten or fifteen minutes after its initiation the conidium has attained more than half its mature size (PLATE 30, FIGS. 14, 15). A definite sequence of events now follows: the nucleus passes into the spore, the conidial membrane thickens, and the circle of attachment between spore and conidiophore becomes differentiated as a short collar (the basidium of some writers), narrower than the rest of the conidiophore. A thin wall forms across the base of the spore, separating its contents from the conidiophore, which now also forms a limiting cross wall in close apposition to the conidial cross wall. Until this occurs, the pro-

toplasm has had free ingress to the enlarging spore; with the closing of this entrance, pressure within the conidiophore is increased, so that the two cross walls are forced convexly into the spore, and the attachment between conidium and conidiophore is ruptured in a ring around the base of the former. The spore is at once violently discharged, so swiftly that its flight, as seen through the microscope, is like a flash of light. Obviously, the flight is too rapid for details to be observed; but as the conidium comes to rest upon the cover glass, it can be seen that the end which was attached is now everted to form the tapering base of the spore, marked, where it was torn loose from its attachment, by a roughened external ring. Of the several forces operative in the discharge of the conidium, the writer believes that the most potent is the recoil of this basal wall, which acts as a spring to push the spore into space as soon as the circle of attachment to the conidiophore is broken by the pressure within the latter.

The behavior of the conidiophore and its content varies considerably in the period concurrent with, and immediately after, the projection of the spore. Usually the sudden release of pressure causes the thin elastic membrane across the neck of the conidiophore to stretch abruptly, and as rapidly to contract, so that the protoplasm rushes forth to form momentarily a terminal globule, which as quickly retreats within the conidiophore; the latter is thus left turgid and normal in appearance except for a slight infolding at the tip (PLATE 30, FIGS. 24, 25). Sometimes the conidiophore and its terminal membrane are so stretched that some of the elasticity is lost, and only partial withdrawal of the conidiophore content is effected. Again, there may be a weak discharge of the conidium with no emergence of protoplasm from the conidiophore.

The writer has observed many conidiophores in the act of spore discharge, and in no case has there been an actual loss of content; in those cases in which the protoplasm emerges, whether abruptly or slowly, the terminal membrane of the conidiophore, although it may stretch greatly, always remains unbroken, and the content is completely or partially withdrawn.

Although processes in the normal formation of the conidia

may best be observed in highly humid air, as outlined above, study of conidiophores mounted in water is also helpful. In plate 30, figure 19 may be seen a nearly full-grown conidium in which the basal cross wall is beginning to form; the latter appears in optical section as a shelf-like projection from either side. Centripetal development of this wall results in a complete separation of spore content from conidiophore protoplasm, as seen in figure 20. Olive (11) has described the formation of cross walls in the Entomophthoraceae by centripetal development, but the cleavage furrow which he emphasized was not observed in this case. In figure 21, the protoplasmic pressure within the conidiophore has pushed the walls convexly into the spore; and in figure 22, two walls, the basal septum of the spore and the terminal septum of the conidiophore, may be plainly seen. Sections of fixed and stained material have also been observed, but were found inferior to fresh, living material.

Investigators have expressed different opinions regarding conidial formation in the Entomophthoraceae. Thus Thaxter (l.c., pp. 143-144) regards the conidium as a one-spored sporangium; the wall of the protuberant conidiophore tip thus functions as a sporangial wall, within which the single spore differentiates, and the terminal membrane of the conidiophore becomes a true columella. All attempts by the writer to demonstrate a double character of the conidial wall have failed, and he believes that the *Entomophthora* conidium is not a sporangiospore. Both Thaxter (l.c.) and Vuillemin (17), however, have described conditions in which an outer (sporangial) wall was separated and plainly distinguishable from the spore wall. The former has described and figured (l.c., figs. 320, 321) conidia of *Empusa sepulchralis* in which absorption of water had caused a wide separation of the two walls, and the spore is apparently floating freely within a sporangium; see text figure B, 6, 7. Vuillemin (l.c.) in describing a new species, *Entomophthora gloeospora*, placed considerable emphasis on a condition (TEXT FIGURE D, 1-3) observed during spore formation as well as in the ripe spore, in which there is a distinct gelatinous layer between the outer surface of the conidium proper and the episporule (sporangial wall). He distinctly states that this is not a gelatini-

zation of the spore wall, and that the episporic is a separate membrane. On the basis of this gelatinous coat and its limiting membrane, Vuillemin would regard *Entomophthora gloeospora* as "a transition form between the clearly exogenous conidia of the Entomophthoraceae and the sporangia of the Mucorineae."

In conidia of *Entomophthora sphaerosperma* treated with soap solution (TEXT FIGURE E, 1-3) and occasionally even in untreated spores, the writer has observed a condition strikingly similar to the conditions figured by Thaxter and Vuillemin, as described above. In this case, however, the enveloping substance is not a sporangial wall, for it usually does not completely enclose the spore; and furthermore, it sometimes does not occur at all. Moreover, the writer has never been able to observe this substance while the conidium is still attached to the conidiophore. In the case of *Entomophthora sphaerosperma*, at least, this spore envelope is a much swollen condition of the gelatinous apical cap described earlier in this paper. The conidia of all the Entomophthoraceae are markedly adhesive, and it is probable that in the presence of slight moisture there occurs a thin and usually imperceptible layer of this gelatinous material on the conidial surface, which in certain species occasionally becomes developed in sufficient amount to become readily visible.

In the matter of conidial discharge also there has been some difference of opinion. Brefeld (3), for example, who has also described the discharge of conidia of *Entomophthora sphaerosperma*, and whose observations are diagrammatically represented in text figure C, 1-3, states that there is a single septum, the basal membrane of the conidium, which is at first pushed convexly into the conidiophore and later arches out into the conidium. When the spore is freed from the conidiophore by circumferential rupture at its base, it is violently discharged, together with the content of the conidiophore; thus the spore becomes coated with protoplasm, which can be seen clinging to the conidial surface in a freshly shot-off spore. The writer has already made it clear that he has never seen an actual loss of protoplasm from the conidiophore; however, he has also emphasized the differences in behavior exhibited by the conidiophore and its content after spore discharge, and it is entirely possible

that under certain conditions the conidiophore membrane may burst and the entire content be discharged, in which case the spore might become coated with protoplasm and the conidiophore left in the shriveled condition which Brefeld describes. Indeed, it is very probable that the widely different details of spore discharge described for different species of the Entomophthoraceae are largely due to different conditions under which they were observed, rather than to errors in observation or inherent differences in the fungi.

*B. GERMINATION.* Conidia vary in their manner of germination. In water or in humid air a stout germ tube is usually formed (PLATE 30, FIGS. 27-31; 35, 36); sometimes, however, the tube grows vertically and functions as a conidiophore, at whose tip a secondary conidium is formed, precisely like its antecedent except for a slight diminution in size (PLATE 30, FIGS. 32-34).

The secondary conidium is abstracted in the usual manner and may likewise give rise to a tertiary conidium, and so on, until vitality is exhausted or, perchance, an opportunity is afforded for infection. Sometimes the secondary conidium is produced at the tip of a long and extraordinarily thin germ tube (PLATE 30, FIGS. 38-40). This capillary type of conidiophore has been figured by Thaxter (l.c.) for six species including *Entomophthora sphaerosperma*, and seems to belong especially to those forms with relatively small and elongate conidia of the *Entomophthora sphaerosperma* type.

Germination begins with a slight outward bulging of the conidium at any point on its surface, and rapidly proceeds to tube formation. The tube wall differs from the spore wall only in being slightly thinner. The protoplasm, too, is unchanged, except for more vacuolation. The nucleus does not divide until it has migrated into the tube, and, in the cases observed, when a secondary spore is to be formed, the nucleus does not divide at all. Thus the secondary spore has the same nucleus and cytoplasm as did the primary conidium, and it is probable that this condition holds throughout the entire series of secondary spores formed.

When germination takes place in water or air, no food is avail-

able and thus it follows that as the germ tube elongates beyond the expansibility of its protoplasmic content, the latter is carried along in the advancing tip, leaving a vacant area behind. This retreating protoplasm may form a cross wall at its rear and again withdraw, and so a series of empty compartments may occur in the germ tube behind the relatively short terminal space filled with protoplasm (PLATE 30, FIG. 37).

A relative humidity of at least 70 per cent is essential to germination, and the most favorable temperature is near 20° C., when conidia will send forth germ tubes two hours after formation. Spores will not germinate at temperatures of 26° C. or above. Low temperatures retard, but do not prevent, germination; for, as explained in a previous paper (l.c.), conidia remain dormant in ice for at least a week and then germinate readily upon return to favorable temperatures. It is of some interest to note that low temperature (8° C.) during germination results in the formation chiefly of secondary conidia on capillary conidiophores; that this is an effect of low temperature during, and not previous to, germination is shown by the fact that spores which have been frozen and then brought to a temperature near 20° C. form the usual germ tubes, instead of capillary conidiophores.

Light also affects germination. In darkness more conidia germinate than in light and relatively fewer capillary conidiophores occur. The writer has noted that conidia, unless rendered dormant by low temperature as noted above, must germinate at once after their formation or else die. This observation is not in agreement with Brefeld's (4) statement that conidia of this species remain viable for eight days after production.

2. *Mycelium*. Upon proper nutrient media, germ tubes may continue to develop, building up an extensive, branched mycelium (PLATE 31, FIGS. 4, 5). The hyphal walls are thin and the protoplasm finely and evenly granular, with occasional vacuoles. Cross walls do not normally occur in the hyphae unless the latter are about to segment into hyphal bodies, but it has been found in artificial culture that their production may be induced by depletion of the food supply. Nuclei are numerous. Frequently they are evenly spaced in linear sequence; often, however, they occur in pairs, in the same oblique position in which division occurs.

3. *Hyphal bodies.* The mature mycelium segments into the characteristic short individual pieces named by Thaxter *hyphal bodies*. Stages in their formation, as observed by the writer, are as follows: a delicate cross wall begins at the periphery of the hypha and develops centripetally. This wall is thin, single, and unaccompanied by the cleavage furrow described by Olive (l.c.). Usually it develops along the border of a large vacuole, which thereby becomes flattened transversely to the hypha (PLATE 31, FIGS. 7, 8); wall formation through a vacuole has, however, also been observed. The protoplasm then cleaves away from one side of the completed cross wall and the tubular wall of the hypha breaks (PLATE 31, FIG. 9), thus completing the segmentation. It is noteworthy that the transverse wall does not appear to split, but the protoplasm withdraws slightly from one side, so that after the hyphal pieces separate, the protoplasm is restrained in one segment by the transverse wall and in the opposed end of the adjacent segment by the plasma membrane, which may subsequently become slightly thickened. The writer has also seen infected insect larvae in which regions of the invading mycelium had become much attenuated (PLATE 31, FIG. 5) and it is possible that hyphal bodies may sometimes arise through completion of such constrictions.

Old hyphal bodies are prone to form short branches and twist into irregular shapes, while the content becomes less vacuolate, condensed, and coarsely granular (PLATE 31, FIGS. 12-14). Spherical and ovoid forms, often with one or more large central vacuoles (PLATE 31, FIGS. 15-17), consistently occur in old cultures on swordfish. Indeed, the hyphal bodies show all stages in variation between mycelial structures and spherical, spore-like bodies.

4. *Rhizoids.* *Rhopobota* larvae infected with *Entomophthora sphaerosperma* show a remarkable indifference to the progress of the disease, and death does not occur until most of the body tissues are in a marked state of disintegration. About the time the insect dies, some of the hyphae in the thoracic region aggregate and push through the ventral surface of the host as stout tubular structures, which attach the host firmly to the substratum; these are the rhizoids (PLATE 31, FIG. 40) and con-

stitute the only phase in the life cycle of this fungus which is not developed upon artificial culture media.

Each rhizoid consists of many straight, parallel, unbranched hyphae; the presence of bubbles along the lumen when the rhizoid is immersed in water shows clearly that these hyphae are arranged in tubular formation. Where the distal end comes in contact with a solid surface, the individual hyphal ends fan out into a funnel-like, closely appressed mouth, which anchors the insect securely to the substratum (PLATE 31, FIG. 40). For some reason, perhaps because internal development is more advanced in this region, the rhizoids always appear first (in varying numbers) between the thoracic appendages. Their appearance is indicative of the completion of vegetative growth within the host, and this phase is soon followed by conidiophores or by the internal development of resting spores.

5. *Conidiophores*. The conidiophores branch from the hyphal bodies, or, if they develop early, from unsegmented hyphae. The protoplasm often shows streaming movements; nuclear divisions are frequent and nuclei are comparatively abundant. Growth is rapid and the conidiophore may attain full development and begin to liberate ripe conidia within five hours after its initiation.

The writer has not attempted to study the cytology of this species in detail; the frequent nuclear divisions in the conidiophores do, however, make the latter an especially favorable phase in which to observe mitotic behavior, and such details as have been encountered in the general study of the conidiophores will be described at this point.

The resting nuclei are 3 to 4  $\mu$  in diameter. They have a well-defined enveloping membrane and dense, finely granular content. The deep-staining reaction of the granules indicates that they are chromatin; no achromatin network was observed. One to several nucleoli occur, two being the usual number. The nuclear structures stain very well with Haidenhain's haematoxylin; after considerable differentiation in iron-alum solution, the nuclear membrane, chromatin granules, and nucleoli stand out in deep black against the light gray of the surrounding cytoplasm (PLATE 31, FIG. 18).

A definite spireme could not be observed in the prophase; instead, the chromatin aggregates into larger granules to form the individual chromosomes (PLATE 31, FIGS. 35-37), whose number appears to be twelve or more. The nuclear membrane persists until division is completed and the mitotic figures are therefore intranuclear. The chromosomes crowd together in the center of the nucleus into a dense mass in which the individual units are not entirely discernible, and numerous delicate, but well-defined spindle fibres appear (PLATE 31, FIG. 32). The mass of chromosomes now separates into two groups, which begin their migration to the opposite nuclear poles (PLATE 31, FIG. 33). In plate 31, figure 34, may be seen a pair of nuclei that have developed simultaneously; it will be noted that although this is a telophase stage, the nuclear membrane is still intact. This habit of simultaneous division of paired nuclei is of too frequent occurrence to be accidental. Stages in the reconstruction of the resting nucleus were not observed. These steps in mitosis as seen by the writer show close similarity to those described by Riddle (12) for nuclear division in *Entomophthora americana*, with, however, one outstanding difference: the nucleolus in *Entomophthora sphaerosperma* does not become one of the chromosomes, but remains clearly distinguishable from them (PLATE 31, FIG. 37).

Following this initial period of active protoplasmic increase and nuclear multiplication, the nuclei become more widely spaced and the cytoplasm becomes less dense and more vacuolate. From these facts it would appear that the later development of the conidiophore and its conidium is largely dependent on absorption of water.

The conidiophores have a tendency, both in culture and on the host, to aggregate in clumps (PLATE 30, FIG. 1), and although their tops may coalesce to form an uninterrupted surface, these groups retain their individuality throughout the several hours (or days, if environmental conditions are favorable) that they persist. Further details of conidiophore structure have already been described under the discussion of conidia. Sterile conidiophores, interspersed with normal ones, have been noted in some cases (PLATE 30, FIG. 41) upon insects, but never in culture.

6. *Resting spores.* Hyphal bodies may form resting spores, instead of conidiophores; their simultaneous appearance is rare in the insect host, but may be easily brought about in culture by the use of suitable media, such as yolk of egg. The resting spore begins as a protuberance from the end or side of the hyphal body (PLATE 31, FIGS. 20-28), into which cytoplasm and nuclei migrate, leaving the hyphal body partially or completely emptied of its content; usually cross walls are formed behind the retreating protoplasm, as already described in the case of conidial germ tubes. The number of nuclei varies; usually from fifteen to twenty enter each spore. Sections of mature resting spores show as many nuclei, on the average, as do young spores, and it may therefore be assumed that no nuclear fusion takes place, at least during the formation of the spore; Riddle and others have stated for another species that no fusion had occurred in resting spores several weeks, or even months, old.

After the protoplasm has entered the young spore, it is cut off by a thin wall, continuous with the wall of the hyphal body. As the spore matures, this wall thickens somewhat to become the epispore, while the peripheral portion of the enclosed protoplasm secretes the still thicker endospore; the exact steps in the formation of the latter cannot be clearly seen.

Almost as soon as the protoplasm enters the spore from the hyphal body, it becomes denser and less vacuolate, and this condensation continues until, when full grown, the spore is closely packed with coarse granular protoplasm. As the spore ripens, oil globules begin to appear, at first small and numerous, but soon coalescing, until sometimes a single large refractive globule remains, suspended in a protoplasm now clear and homogeneous (PLATE 31, FIGS. 28-31). The development of the resting spore requires about forty-eight hours; final stages in ripening may be hastened by placing the spores in water. The mature spores are spherical and average  $15 \mu$  in diameter.

Digression may be made here to consider briefly certain factors influencing the formation of resting spores. Brefeld, in his researches upon *Entomophthora sphaerosperma*, found, both in nature and in a series of artificial inoculations extending over several weeks, that cabbage-worms containing resting spores, as

compared with those on which conidia were formed, were more numerous as summer progressed into autumn. From this observation he concluded that the resting spore is an adaptation for hibernation, and this theory has led to the general conclusion that the formation of resting spores in the Entomophthoraceae is a result of low temperatures. Thaxter (l.c., p. 150), however, has pointed out that as many infected insects contain resting spores in mid-June as in mid-October, and the writer has found this to be true of *Rhopobota vacciniana*. Indeed, resting spores developed in nearly all infected fireworms kept in the laboratory in early summer, while infected larvae out-of-doors, so far as could be detected, were giving rise only to conidia. The environmental factors that differed in the two cases seemed chiefly to be those of light and temperature, for the experimental larvae in question were in the dark and subjected to a temperature, especially during the night, which was several degrees above the temperature on the cranberry bogs. This led the writer to keep some larvae in the dark and others in light at the same temperature, while two other lots were kept in darkness at different temperatures, one from 12° C. to 16° C., the other from 25° C. to 30° C.

Resting spores were formed in the same number of larvae in light as in darkness, and therefore it would seem that light is not the factor that determines their formation; these observations do not agree with Speare's (15) upon *Entomophthora Pseudococci*, in which he states that hyphal bodies form conidio-phores when subjected to light, and resting spores when kept in the dark.

The effect of temperature, however, was quite different, for of the larvae kept at 25° C. to 30° C., more than three times as many contained resting spores as did at the lower temperature; it is perhaps noteworthy that at the same time no conidia occurred at 25° C. to 30° C., although they were formed profusely at 12° C. to 16° C. Furthermore, in artificial culture upon potato, it has not been possible to obtain resting spores of *Entomophthora sphaerosperma* at temperatures of 21° C. or below; but when such cultures are kept at 27° C., for forty-eight hours or more, resting spores are formed in profusion.

These facts are strongly indicative that temperatures above the optimum for growth are, contrary to usual opinion, more favorable for the production of resting spores than lower tem-

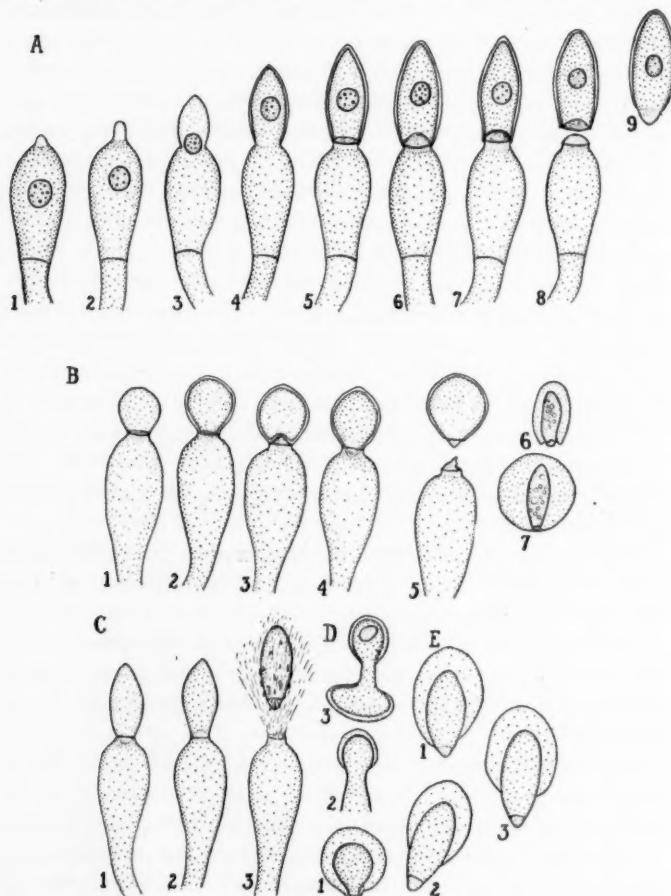


FIG. 1.

peratures. That temperature is not the only factor that may be concerned, however, is indicated by the fact that resting spores of *Entomophthora sphaerosperma* are readily formed upon egg

yolk at 20° C., while, as noted above, a higher temperature is necessary for their production on potato media. Perhaps resting spore formation depends upon a particular mode of protoplasmic activity which in one case is initiated by high temperature, and in the other by chemical "activators" present in egg yolk and absent in potato.

The question of a sexual process in this fungus remains for discussion. In a few species of Entomophthoraceae, the sexual origin of the resting spores has been clearly demonstrated, and beyond doubt they are zygospores. In other cases, the spores as obviously develop without conjugation, and are azygospores. In still other species the origin is not clear, but suggests a possibility of a conjugation of hyphal bodies prior to spore formation; *Entomophthora sphaerosperma* belongs among these doubtful forms, for Brefeld (4) described anastomoses of hyphae before the resting spores were formed, but could not associate these unions with individual spores, and Thaxter (l.c.) has described and figured instances that strongly suggest, but do not prove, the conjugation of hyphal bodies in relation to spore formation.

The writer regrets that he is unable to fulfill Lakon's (9) prediction that when *Entomophthora sphaerosperma* could be grown in artificial culture, the sexual origin of its resting spores would be clearly demonstrable. In the great majority of cases, the resting spores are very clearly azygospores (PLATE 31, FIGS. 22-24). Occasionally, however, diligent search will reveal a condition such as is shown in plate 31, figures 27 and 28, which are of the same spore, as seen from opposite sides, which might be interpreted as representing conjugation prior to the formation of the spore. The writer has been totally unable, however, to find any case which could not as readily be interpreted as due to septum formation, a regular incident of spore production in this species. In view of the fact that a thorough examination of countless resting spores has never revealed a clear case of sexuality, and even the doubtful cases are very rare as compared with the definite instances of asexual origin, together with the fact that the structure suggesting conjugation may, in every case seen, as readily be interpreted as an ordinary vegetative cross wall, the writer is of the opinion that the origin of resting spores

in this species is non-sexual, and that they are always azygospores.

Every attempt to bring about germination of the azygospores of *Entomophthora sphaerosperma* has failed, although freezing, drying, heating, treatment with acid, and other measures have been tried. Spores have even been kept out-of-doors for a whole year, under conditions which duplicated those in nature, and although they were frequently examined, germination was never observed.

Gilliatt (8) has recorded germination of the resting spores of *Entomophthora sphaerosperma* in water sixteen days after their suspension in Van Tieghem cells. These experiments were repeated by the writer with azygospores, both from insect larvae and from artificial culture, but germination did not occur. Gilliatt, in those cases where germination took place, neither figured nor described the thick double wall characteristic of true resting spores, and his figures suggest germinating hyphal bodies. Indeed, the writer has yet to be convinced that an authentic case of germination of true resting spores (zygospores or azygospores) has ever been observed in any member of the entomogenous Entomophthoraceae; in no case reported is there definite evidence, either from description or figures, that hyphal bodies were not the structures concerned.

The stages in the life cycle of this fungus as described above (with the exception of the rhizoids) have been studied both in the host and in artificial culture, and have been found to agree in all essential details.

The writer wishes to express to the President and Governing Board of Bates College his appreciation for the leave of absence which made this work possible, and to Professor William H. Weston, Jr., grateful acknowledgment of his never-failing encouragement and inspiration.

#### SUMMARY

1. Cultivation of *Entomophthora sphaerosperma* on artificial media has made a detailed study of this entomogenous fungus possible.

2. The single spores are true conidia, in that they are not formed within a separable sporangium.
3. The forcible projection of the conidium from the conidiophore is due to a definite chain of occurrences, chief among which are swelling of the conidiophore, circumferential rupture of the attachment around its tip, and a recoil of the spore's basal membrane.
4. The conidium possesses a gelatinous apical cap, which aids in its attachment to the host.
5. Conditions most favorable for spore germination are a temperature of 20° C., a relative humidity of 70 per cent or more, and darkness. Conidia are not injured by freezing.
6. Rhizoids are not formed in artificial culture; all other phases of the life cycle are the same in artificial culture as in the insect host.
7. During mitosis, the nuclear membrane persists until the telophase. Definite chromosomes, at least twelve in number, are formed. A well-defined spindle exists and one or more nucleoli are present throughout division, distinct from the chromosomes.
8. Resting spores in this species are formed asexually and are therefore azygospores. Their formation is subject to artificial control in which the determining factors may be either temperature or special artificial media.

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#### EXPLANATION OF PLATES

##### PLATE 30

*Entomophthora sphaerosperma*. Conidia, conidiophores, and hyphal bodies.

Fig. 1. A typical group of conidiophores on the surface of the host, showing their interwoven bases, the habit of branching, and conidia. Semi-diagrammatic,  $\times 15$ ; Fig. 2. Two conidiophores, more in detail, separated from a group similar to that shown in fig. 1,  $\times 230$ ; Fig. 3. A young conidiophore. Note the vacuolate cytoplasm, the numerous nuclei, the branches, and a conidium forming at the tip,  $\times 470$ ; Figs. 4-8. Conidia stained with weak safranin-glycerine. The elliptical shape, papillate base, finely reticulate cytoplasm, and single central nucleus with nucleoli and chromatin granules may all be noted,  $\times 830$ ; Figs. 9-11. As above; also a cap-like outer layer of gelatinous material is shown in different stages of development. In fig. 10,

this cap has been displaced to one side,  $\times 830$ ; Figs. 12-18. Successive stages in development of the same conidium at known time intervals: fig. 12 shows the conidium initial just forming at 11:10 p.m.; figs. 13-16 indicate stages in growth at 11:15, 11:20, 11:25, and 11:30 p.m., respectively; fig. 17, at 11:45 p.m., shows the differentiation of a collar-like portion ("basidium") at the top of the conidiophore, the thickening of the wall of the conidium, and the wall formed across its base; fig. 18, at 12:05 a.m., shows the cross wall pushed up into the conidium by pressure of the protoplasm in the conidiophore. This spore was shot off two or three minutes later,  $\times 1000$ ; Figs. 19-22. Conidia in different stages of development, mounted in water and viewed with oil immersion objective. Fig. 19 is of a conidium and conidiophore with a large vacuole in each; note especially the early stage in centripetal development of the conidial cross wall. In fig. 20, this wall is completed. In fig. 21, the wall has become forced convexly into the spore. In fig. 22, two cross walls are present in close apposition, one belonging to the conidiophore and the other to the spore, and both pushed upward; the conidiophore and conidium are thus in the ball-and-socket relation which is attained just before discharge,  $\times 1000$ ; Fig. 23. A conidiophore after discharge of the spore,  $\times 1000$ ; Figs. 24-26. Stages immediately following spore discharge, showing formation of a protoplasmic vesicle and its withdrawal,  $\times 1000$ ; Figs. 27-31. Conidia germinating in water. The large vacuoles and stout germ tubes should be noted,  $\times 1000$ ; Figs. 32-36. Conidia germinating in moist air; figs. 32-34 are stages in the formation of secondary conidia; figs. 35-36 are of conidia forming germ tubes; note the large vacuole in the conidium in fig. 35, and the emptied spore in fig. 36,  $\times 1000$ ; Fig. 37. A condition similar to that in fig. 36, but further advanced; the protoplasm is all in the tip of the germ tube, and the rest of the tube is separated into compartments by cross walls,  $\times 1000$ ; Figs. 38-40. Conidia with capillary conidiophores and secondary conidia,  $\times 1000$ ; Fig. 41. Sterile conidiophores from the midst of normal fertile conidiophores on fireworm,  $\times 470$ ; Figs. 42-43. Young hyphal bodies,  $\times 470$ .

## PLATE 31

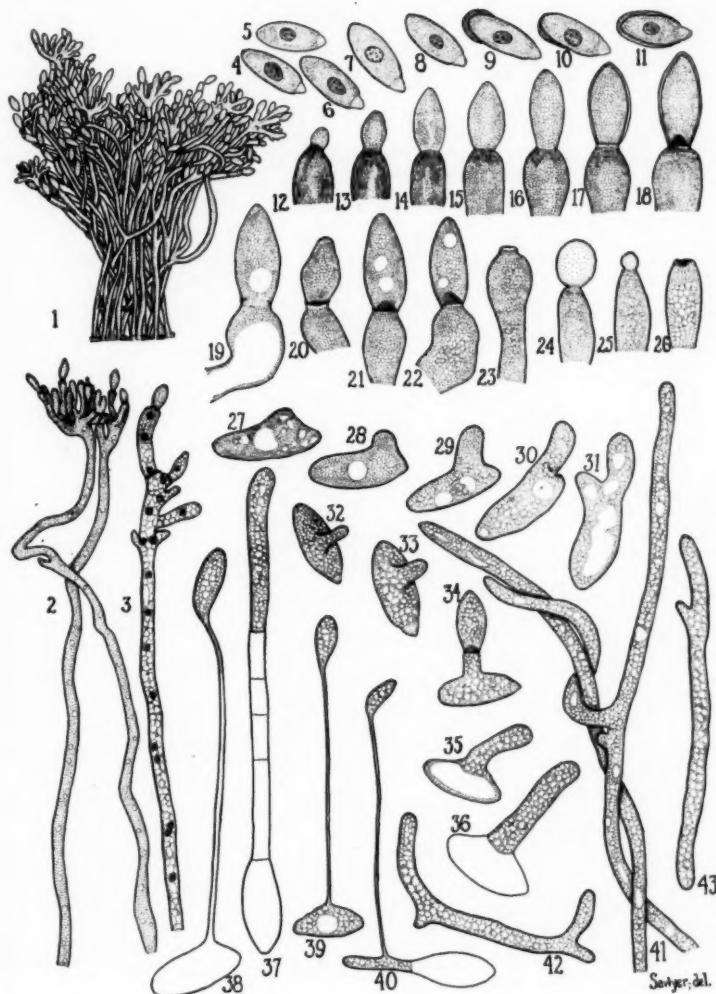
*Entomophthora sphaerosperma*: penetrating germ tubes, mycelium, hyphal bodies, rhizoids, conidiophores, and resting spores.

Figs. 1-3. Conidial germ tubes penetrating the body wall of the host. In figs. 1-2, the conidium has lodged endwise among the cuticular spines and germinated from the apical end, penetrating the primary cuticle and invading the secondary cuticular layer. The germ tube in fig. 2 has branched. In fig. 3, the conidium has germinated in a mass of conidia and debris some distance away and the germ tube has grown to, and penetrated the body wall as far as the hypodermis,  $\times 1000$ ; Fig. 4. A hypha obtained by crushing the body of an artificially inoculated living fireworm. Note the separation in the protoplasm at the bases of the branches, where segmentation into hyphal bodies was probably about to occur,  $\times 230$ ; Fig. 5. Mycelium similarly obtained. The very attenuated condition of two hyphae suggests that hyphal bodies may sometimes be formed by constriction,  $\times 230$ ; Fig. 6. A hyphal body with much convoluted branch,  $\times 230$ ; Figs. 7-10. Stages in segmentation to form hyphal bodies. In fig. 7, a cross wall has formed in

connection with a vacuole; fig. 8, a similar condition which shows the cross wall pressed in upon the vacuole; fig. 9 is of a stage immediately after segmentation of the hypha; the broken ends of the hyphal wall at the point of segmentation, the terminal cross wall in one segment, and the corresponding plasma membrane in the other, may all be seen. Fig. 10 represents a later condition in which one of the segments has branched, forming one of the elbow-shaped hyphal bodies common in these fungi,  $\times 700$ ; Fig. 11. Hyphal body showing nuclei, often in pairs, and the somewhat vacuolate cytoplasm containing deeply staining granules of reserve food material,  $\times 700$ ; Figs. 12-14. Hyphal bodies: fig. 12, from host; figs. 13-14, from potato culture,  $\times 300$ ; Figs. 15-17. Rounded vacuolate hyphal bodies from old swordfish culture,  $\times 300$ ; Fig. 18. Young conidiophore arising as a branch from a small hyphal body. Note the frequent paired arrangement of nuclei,  $\times 700$ ; Fig. 19. Two hyphal bodies overlapping, so that they simulate a condition of conjugation, which, however, is not taking place,  $\times 300$ ; Figs. 20-28. Stages in formation of resting spores. In fig. 20, the spore has begun to form as an enlargement of the end of the hyphal body. The two nuclei in the young spore are merely in contact, not fusing,  $\times 700$ . Figs. 21-23 show resting spores arising terminally; figs. 24-25, laterally. Fig. 26 shows a laterally-formed resting spore on an unusually large hyphal body. Note the separation of protoplasm at the base of the spore, preparatory to wall formation. Figs. 27-28 represent opposite sides of a resting spore which might have been formed as a result of conjugation; it is probable, however, that this appearance is due to a cross wall laid down in the single hyphal body from which the spore arose laterally. In fig. 23, oil globules may be noted, present at an unusually early stage in spore development. Also note that it is usual for cross walls to form in the hyphal bodies as the protoplasm migrates into the growing resting spore,  $\times 300$ ; Figs. 29-31. Ripe resting spores from egg yolk culture. In fig. 29 ( $\times 700$ ) the thick double wall and the numerous oil globules suspended in a clear, homogeneous protoplasm may be noted. Figs. 30-31 ( $\times 880$ ) show a condition in which the oil is aggregated into a few large globules; in fig. 31, the point of attachment to the hyphal body may be seen; Figs. 32-37. These represent phases in nuclear behavior during division. Fig. 32 shows a lateral view of a metaphase stage, with a well-defined spindle and the chromosomes closely compacted in the equatorial plate. The cytoplasm contains densely staining food granules. In fig. 33, an anaphase is shown, soon after division of the chromosomes which are too compacted to permit counting. In fig. 34, a later stage, a pair of nuclei have divided simultaneously. Fig. 35 shows nuclei cut somewhat tangentially, and including but a few chromosomes. Figs. 36-37 show more nearly median sections of nuclei in which the chromosomes are distinct, and also, in fig. 37, a large nucleolus, easily distinguishable from the chromosomes in the same nucleus,  $\times 1600$ ; Fig. 38. Penetration of muscle by hyphae. Note attenuation of hypha where the muscle is penetrated and the space formed on either side of the hypha by enzymic dissolution of the muscle tissue,  $\times 300$ ; Fig. 39. Hypha penetrating cell in wall of stomach,  $\times 300$ ; Fig. 40. Rhizoids emerging through body wall in the mid-ventral thoracic region of the host. Note their branching character, their composition of parallel hyphae, the funnel-like holdfast, and their size as compared with the vegetative hyphae protruding from beneath the cuticle,  $\times 50$ .

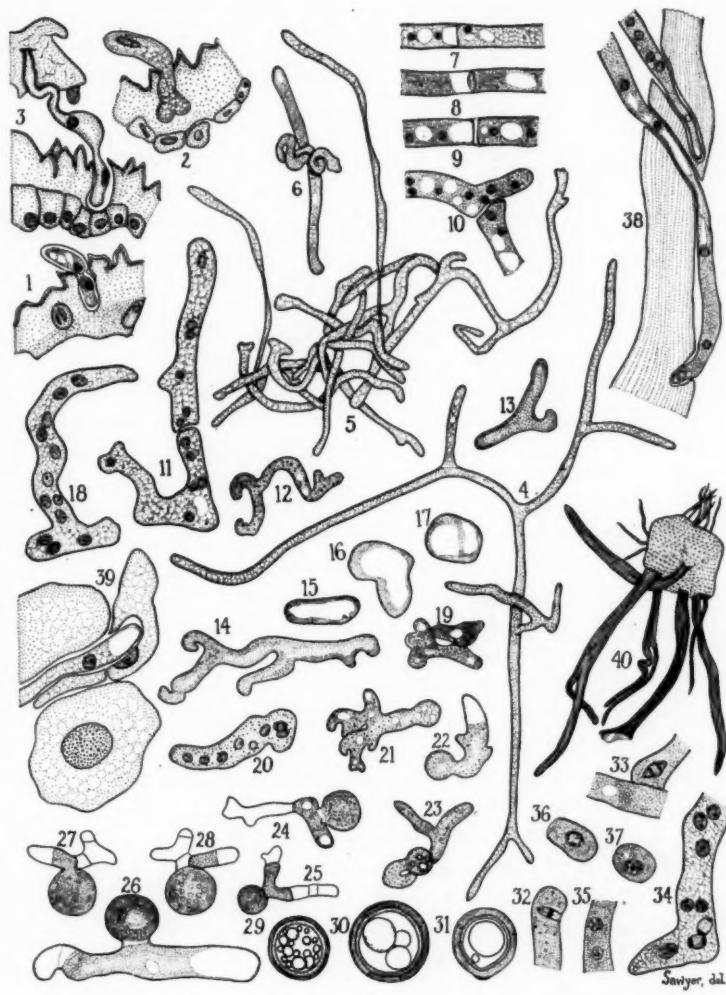
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## ENTOMOPHTHORA SPHAEROSPERMA





ENTOMOPHTHORA SPHAEKORUM

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## PHRAGMIDIUM SPECIES OF NORTH AMERICA: DIFFERENTIAL TELIOSPORE AND AECIAL CHARACTERS<sup>1</sup>

GEORGE B. CUMMINS<sup>2</sup>

(WITH PLATE 32)

Differential teliospore characters of the nineteen species of *Phragmidium* in North America are used herein as a basis for arranging the species occurring on the three host tribes, Potentilleae, Rubeae and Roseae, under the two sections of the genus *Phragmidium*, *Earlea*, characterized by firm non-hygroscopic teliospore pedicels, and *Euphragmidium*, characterized by hygroscopic teliospore pedicels. Aecial characters and teliospore characters are used as bases for keys to the species on each of the three host tribes. For host range and geographic distribution of each species the reader is referred to the North American Flora (3). Measurements are included where they are useful and when pertaining to teliospores do not include the pedicels.

The first comprehensive study of the rust genus *Phragmidium* was published by Dietel (4) in 1904. In this paper he recognized seventeen species in North America and of this number thirteen are accepted as valid today. Arthur (1), in 1906, erected the genus *Earlea* to provide for those species which lacked uredinia in the life-cycle and in 1912 followed the same arrangement in the North American Flora (3). In subsequent works by Sydow (6) and Dietel (5) this separation into two genera was not accepted.

<sup>1</sup> Contribution from the Botany Department, Purdue University Agricultural Experiment Station, Lafayette, Ind.

<sup>2</sup> The writer wishes especially to thank Dr. J. C. Arthur for helpful suggestions and criticism during the course of the study, and for the privilege of using the scheme of sections as set forth in his unpublished manuscript.

### SECTIONS EARLEA AND EUPHRAGMIDIUM BASED ON NATURE OF TELIOSPORE PEDICELS

During the course of this study it has been the writer's privilege to consult the unpublished manuscript of a rust manual prepared by Dr. Arthur in which he divides the genus *Phragmidium* into two sections, *Earlea*, consisting of the species with firm non-hygroscopic teliospore pedicels, and *Euphragmidium*, consisting of the species with hygroscopic pedicels. This subordination of his previously erected genus *Earlea* is based on the fact that the uredinia belong to the same vegetative phase (diploid) as the telia and their presence or absence is considered insufficient basis for generic distinction. The nineteen species to be discussed in this paper will be arranged, with few modifications, in accordance with this scheme.

According to this arrangement there are on Potentilleae two species under *Euphragmidium* and four species under *Earlea*. This places *Phragmidium Potentillae* (Pers.) P. Karst. under the section *Earlea*, a procedure not previously suggested. While uredinia occur regularly in the life-cycle, other characters, such as the non-hygroscopic pedicel, the smooth spore-wall and the absence of a well-defined apiculus on the teliospores, indicate that the affinities of this species are with the *Earlea* section. In the group on Rubeae four species are in the section *Euphragmidium* and one in *Earlea*, and of the eight species on Roseae only one is under *Earlea*.

#### AECIAL CHARACTERS OF THE NORTH AMERICAN SPECIES

A critical study of the aeciospores shows that in these, also, there is a segregation into two distinct divisions based on the spore markings, divisions which do not, however, coincide with the sections *Earlea* and *Euphragmidium*. The predominant type of marking may be designated as verrucose with regular papillae. All of the species on Roseae and approximately half of those on Potentilleae and Rubeae have aeciospores of this type. *Phragmidium Rubi-idaei* (DC.) P. Karst. is so sharply papillose that it is more properly classed as strongly echinulate. The second type may be characterized as coarsely verrucose with irregular

warts and presents no gradation into the papillose type in any of the species studied. In the Roseae group it is necessary to take account of the spore wall thickness, the presence or absence of paraphyses, and the effect upon the host, all of which are features subject to some variation.

The determination of species by the examination of a single spore form is sometimes necessary but in general it is possible to collect and examine the other spore forms. When this can be done it will often be found that species with very similar teliospores have aeciospores of very contrasting character. This is especially true of *P. Rubi-idaei* and *P. Rubi-odorati*.

#### CHARACTERS OF THE FOUR SPECIES OF THE SECTION EARLEA ON POTENTILLEAE

In the section *Earlea* the following four species occur on Potentilleae: *P. Potentillae* (Pers.) P. Karst., on *Potentilla* species, *P. Ivesiae* Syd., on species of *Potentilla*, *Ivesia*, and *Horkelia*, *P. biloculare* Diet., on *Potentilla* species, and *P. Horkeliae* Garrett, on *Ivesia Gordonii* (Hook.) T. & G. The teliospores of *P. Potentillae* (PLATE 32, FIG. 9) are smooth and usually 4- to 5-celled and measure 23–30 × 48–89  $\mu$ , but in certain collections may be almost exclusively 3-celled, resembling in this respect *P. Ivesiae* (PLATE 32, FIG. 7) of which, however, the spores are smaller, measuring 19–26 × 35–51  $\mu$ , and the spore wall is verrucose at the apex. Both species have uredinia in the life-cycle. The teliospores of *P. Ivesiae* resemble in size those of *P. biloculare* (PLATE 32, FIG. 8), and *P. Horkeliae* (PLATE 32, FIG. 11), which, however, are 2-celled rather than 3-celled with a chestnut-brown rather than chocolate-brown spore wall. The teliospores of *P. biloculare* are coarsely verrucose with scattered tubercles and can readily be distinguished from the finely and sparsely verrucose spores of *P. Horkeliae*. Neither species produces uredinia.

Aecia are unknown in *P. Horkeliae*. The aeciospores of the other species are very similar, being rather strongly and evenly verrucose with regular papillae. The presence of paraphyses in the aecia of *P. Potentillae* distinguishes this species from *P. Ivesiae* and *P. biloculare* in which paraphyses are wanting. Aeciospore shape is not dependable in separating the latter two

species and it is doubtful whether satisfactory identification on morphologic grounds is possible without examining the teliospores.

#### CHARACTERS OF THE TWO SPECIES OF THE SECTION EUPHRAGMIDIUM ON POTENTILLEAE

The section *Euphragmidium* includes but two species on Potentilleae, *P. Andersoni* Shear, on *Dasiphora fruticosa* (L.) Rydb., and *P. Jonesii* Diet., on species of *Ivesia*, easily separable on either teliospore or aeciospore characters. *P. Andersoni* has 3- to 5-celled, very robust teliospores (PLATE 32, FIG. 10), which terminate in a hyaline papilla, or rarely in a distinct apiculus. In general the teliospore pedicels are one to one and one-half times the length of the spore, with the lower half swelling in water and becoming broadly lanceolate.

*P. Jonesii* has 5- to 9-celled, cylindric teliospores (PLATE 32, FIG. 1) which are somewhat narrowed below and bear at the apex a prominent apiculus. Characteristically the pedicel is shorter than the spore and swells abruptly to fan shape in the lower half, though it may vary, being in rare cases even attenuate.

The aeciospores of *P. Andersoni* are coarsely verrucose with irregular warts while those of *P. Jonesii* (PLATE 32, FIG. 1a) are so finely verrucose with papillae as to appear almost smooth when wet.

#### CHARACTERS OF THE ONE SPECIES OF THE SECTION EARLEA ON RUBEAE

On Rubeae the single representative of the section *Earlea* is *P. alaskanum* (Arth.) Sydow, known only on *Rubus stellatus* Smith, from southern Alaska. The 6- to 8-celled teliospores of this species are cylindric, with an apiculus, and a finely verrucose wall. As in most of the species on Rubeae the aeciospores are coarsely verrucose with irregular warts. There is no other species in North America likely to be confused with this one.

#### CHARACTERS OF THE FOUR SPECIES OF THE SECTION EUPHRAGMIDIUM ON RUBEAE

Four species on Rubeae are included in the section *Euphragmidium*: *P. Peckianum* Arth., on *Oreobatus* species; *P. Rubi-*

*idaei* (DC.) P. Karst., on *Rubus strigosus* Michx., and others; *P. Rubi-odorati* Diet., on *Rubus odoratus* L.; and *P. occidentale* Arth., on *Rubus parviflorus* Nutt. On the basis of teliospore characters alone the separation of certain of the species is difficult but *P. Peckianum* is distinct because the teliospores are only 4-to 6-celled, as contrasted with the 6- to 10-celled spores in the other three species, and are much more robust, tending to be ellipsoid rather than cylindric. The teliospores of *P. occidentale* are the most coarsely marked of any of this group, the markings appearing as prominent, hyaline beads. In relation to spore length the teliospore pedicels in *P. occidentale* are shorter than in *P. Rubi-idaei* or *P. Rubi-odorati*, being about equal to the spore length in *P. occidentale* and nearly one and one-half times the spore length in the other two species. In shape the teliospores of the three species last mentioned are much alike, although those of *P. occidentale* are somewhat narrowed below. The two species *P. Rubi-idaei* and *P. Rubi-odorati*, as will be shown later, are most readily distinguished by the use of aeciospore characters. However, the teliospores of *P. Rubi-idaei* (PLATE 32, FIG. 2) average  $26-30 \times 80-120 \mu$  and are somewhat longer and more slender than those of *P. Rubi-odorati*, which average  $29-34 \times 80-110 \mu$ .

With the exception of one species, the aeciospores of this group are of the type described as verrucose with irregular warts. The exception is *P. Rubi-idaei* the aeciospores of which (PLATE 32, FIG. 2a) are sparsely and strongly echinulate and once seen will be confused with those of no other species in North America. This species is, moreover, the only one in which the aecia are predominantly epiphyllous. Little can be said of the aeciospores of the other three species that is not embodied in the key which is presented later.

#### THE EIGHT SPECIES OF PHRAGMIDIUM ON ROSEAE

Following Dietel (4), Arthur (2) in 1909 published a critical review of the *Phragmidium* species on roses in North America in which he recognized six true members of the genus and in addition included a short discussion of *Phragmidium speciosum* (Fries) Cooke which he at that time considered as in the genus

*Earlea*. The total number of forms in these two genera, which were accorded specific rank, had reached nine at the time Arthur (3) in 1912 completed this section of the Uredinales for the North American Flora. In manuscript he has reduced this number to eight by considering *P. Rosae-setigerae* Diet. as a synonym of *P. americanum* (Peck) Diet., a combination which seems justified.

Morphological characters which can be pointed out as distinctive of any one species, as was possible in the species on *Potentilleae*, are scarce in the forms on *Roseae*. Certain species show marked tendencies in spore shape, size, color, or marking but intergradations are abundant and confusing. A definite knowledge of the host species is more essential here than in the other two groups.

#### CHARACTERS OF THE ONE SPECIES OF THE SECTION EARLEA ON ROSEAE

*P. speciosum* (Fries) Cooke, occurring on many wild and cultivated species of roses, is the sole representative of the section *Earlea* on roses and will, therefore, require little discussion. The teliospores are 4- to 8-celled, with a smooth ashy-brown wall. Typical infections can be recognized without a microscopic examination by the spindle shaped hypertrophy of the stems, bearing felty masses of spores. Aecia occur on leaves and stems, causing a marked distortion of the latter. The aeciospores (PLATE 32, FIG. 13) are thin walled, ellipsoid or more commonly oblong, and large, measuring 18–23 × 26–40  $\mu$ .

#### TELIOSPORE CHARACTERS OF THE SEVEN SPECIES OF THE SECTION EUPHRAGMIDIUM ON ROSEAE

The section *Euphragmidium* includes the following seven species on *Roseae*: *P. Rosae-arkansanae* Diet., on *Rosa arkansana* Porter, *R. Fendleri* Crépin, and *R. suffulta* Greene; *P. disciflorum* (Tode) J. F. James, on *Rosa gallica* L. and *R. alba* L.; *P. Rosae-pimpinellifolia* Diet., on *Rosa eglanteria* L., *R. hemisphaerica* Herrm., and others; *P. Rosae-acicularis* Liro, on *Rosa acicularis* Lindl., *R. nutkana* Presl, and others; *P. montivagum* Arth., on *Rosa Engelmanni* S. Wats., *R. Fendleri* Crépin, and others; *P. americanum* (Peck) Diet., on *Rosa carolina* L., *R. virginiana* Mill.,

*R. setigera* Michx., and others; *P. Rosae-californicae* Diet., on *Rosa californica* Cham. & Schlecht., *R. gymnocarpa* Nutt., *R. nutkana* Presl, and others.

For the species *P. Rosae-arkansanae* and *P. disciflorum*, both with 5- to 8-celled teliospores, the teliospore pedicel is, in typical cases, sufficiently characteristic to separate them from the other five species. The upper half of the pedicel is of uniform diameter and brownish tint. The lower half, however, when mounted in water swells abruptly to clavate or globose, and in *P. disciflorum* (PLATE 32, FIG. 3) characteristically disperses and disappears, often before a mount can be conveniently made and examined. Both have cylindric teliospores rounded at both ends, but those of *P. Rosae-arkansanae* (PLATE 32, FIG. 12) are more robust, measuring 26-29  $\times$  62-80  $\mu$  as opposed to 22-30  $\times$  64-90  $\mu$  in *P. disciflorum*, and the apiculus is very short. In the remaining species the teliospore pedicels swell gradually in the lower half to lanceolate or clavate.

*P. Rosae-pimpinellifoliae* (*P. subcorticium*), with 5- to 7-celled teliospores (PLATE 32, FIG. 4), is the only species on Roseae with spores which deviate strikingly from dark chocolate-brown. The teliospore wall is chestnut-brown and not especially opaque, a character so distinctive that no other need be mentioned. Aside from color the 5- to 9-celled teliospores of *P. montivagum* are similar to those of the preceding species; those of both species measure approximately 24-32  $\times$  64-95  $\mu$  and are rounded above and below.

Of the three species which remain to be discussed *P. Rosae-acicularis* has the smallest and most finely verrucose teliospores (PLATE 32, FIG. 5). The spores are 5- to 11-celled, rather narrowly cylindric, and measure 19-29  $\times$  48-100  $\mu$ . As in the teliospores of *P. Rosae-californicae* those of *P. Rosae-acicularis* tend to be spindle-shaped but the spores taper gradually, both above and below, and the limits of the apiculus can readily be made out. In *P. Rosae-californicae*, however, the spores (PLATE 32, FIG. 6) are strikingly acuminate above, with the apical cell usually much increased in length and grading directly into the apiculus, and the 8- to 11-celled teliospores also are considerably larger (24-32  $\times$  80-130  $\mu$ ).

In *P. americanum* the teliospores are 8- to 11-celled, measure 24–32 × 64–125  $\mu$ , and are cylindric, generally rounded or only slightly narrowed above. In size these approach those of the preceding species but the shape is distinctive and the pedicel is longer, averaging one and one-half times the spore length, while in *P. Rosae-californicae* the pedicel is about equivalent to the spore in length.

#### AECIAL CHARACTERS OF THE SEVEN SPECIES OF THE SECTION EUPHRAGMIDIUM ON ROSEAE

Segregation on the basis of aeciospore markings is not possible in this group, all species having spores of the regularly papillose type. The thickness of the spore wall, a less definite character, serves as a basis for a separation into two groups, one consisting of four species, *P. Rosae-californicae*, *P. Rosae-pimpinellifoliae*, *P. Rosae-acicularis*, and *P. montivagum*, in which the wall is 2–3  $\mu$  thick, and the other of three species, *P. discolorum*, *P. Rosae-arkansanae*, and *P. americanum*, in which the wall is 1–2  $\mu$  thick.

Of the four species with thick aeciospore walls, *P. Rosae-californicae* typically has systemic mycelium, causes marked distortion of the host plant, and has aeciospores (PLATE 32, FIG. 6a) which are large (18–24 × 27–40  $\mu$ ). The aecia of *P. Rosae-pimpinellifoliae* are commonly on the stems but there is no noticeable hypertrophy; the spores (PLATE 32, FIG. 4a) are similar in size to those of the next two species, measuring 13–19 × 19–25  $\mu$ , and paraphyses are few or none. The last character is sufficient to distinguish this species from *P. Rosae-acicularis* and *P. montivagum* which have abundant and conspicuous paraphyses. The separation of the latter two species is more difficult and depends mainly on aeciospore size, those of *P. Rosae-acicularis* (PLATE 32, FIG. 5a) being 18–21 × 24–30  $\mu$ , those of *P. montivagum* 16–19 × 21–26  $\mu$ .

In the group of three species with thin-walled aeciospores, *P. discolorum* is characterized by sparsely and strongly verrucose aeciospores which are relatively large (18–24 × 25–32  $\mu$ ), and by the presence of abundant and conspicuous paraphyses. Paraphyses are present but usually few and inconspicuous in *P. Rosae-*

*arkansanae* and *P. americanum* and the spores measure 16–23  $\times$  20–27  $\mu$ . The aeciospores of *P. Rosae-arkansanae* (PLATE 32, FIG. 12a) are strongly and sparsely verrucose or verrucose-echinulate, while those of *P. americanum* are more closely and finely marked.

#### EFFECT OF THE HOST SPECIES ON SPORE MORPHOLOGY

That the morphology of a species of rust is not unchangeable but is subject to some variation accordingly as it grows on one host species or another is well known and has previously been pointed out by Arthur (2) for certain species of *Phragmidium*, notably *P. montivagum*. The same general phenomenon has been noted in this study in two additional species. Collections of *P. Rosae-arkansanae* on *Rosa Fendleri* Crépin and of *P. Rosae-acicularis* on *R. nutkana* Presl yield teliospores of slightly greater diameter than those on other host species. No significant variation in length of teliospores is evident, the tendency being only to increase a few microns in width with a resulting spore of more robust appearance.

#### KEY TO THE SPECIES OF PHRAGMIDIUM BASED ON AECIAL CHARACTERS

The information derived from these studies of aecial characters in the North American species of *Phragmidium* has added somewhat to the data presented by Arthur (2), in 1909. The artificial key based on aecial characters which follows will perhaps be the most convenient and useful form in which to summarize the present knowledge of the *Phragmidium* species as discussed in this paper.

On the tribe Potentilleae.

- |  |                                     |
|--|-------------------------------------|
| Aecia unknown.   | 1. <i>P. Horkeliae.</i>             |
| Aeciospores verrucose with irregular warts.                | 2. <i>P. Andersoni.</i>             |
| Aeciospores verrucose with regular papillae.               |                                     |
| Aeciospore-wall finely verrucose, appearing almost smooth. | 3. <i>P. Jonesii.</i><br>(Fig. 1a.) |
| Aeciospore-wall sparsely and strongly verrucose.           |                                     |
| Paraphyses present and conspicuous.                        | 4. <i>P. Potentillae.</i>           |

- Paraphyses absent.
- Aeciospores  $18-23 \times 23-26 \mu$ . 5. *P. Ivesiae*.  
(Fig. 7a.)
  - Aeciospores  $16-21 \times 20-30 \mu$ . 6. *P. biloculare*.
- On the tribe Rubeae.
- Aeciospores very strongly echinulate. 7. *P. Rubi-idaei*.  
(Fig. 2a.)
  - Aeciospores verrucose with irregular warts.
    - Aeciospore-wall thin,  $1-1.5 \mu$ . 8. *P. alaskanum*.
    - Aeciospore-wall thick,  $1.5-2.5 \mu$ .
    - Paraphysis-wall thickened above. 9. *P. Rubi-odorati*.  
(Fig. 15.)  - Paraphysis-wall not thickened above.
    - Aeciospores coarsely verrucose. 10. *P. occidentale*.
    - Aeciospores moderately verrucose. 11. *P. Peckianum*.  
(Fig. 14.)
- On the tribe Roseae.
- Aeciospore-wall thin,  $1-2 \mu$ .
  - Aeciospores large,  $18-24 \times 25-35 \mu$ .
  - Aeciospores mostly oblong-ellipsoid. 12. *P. speciosum*.  
(Fig. 13.)
  - Aeciospores mostly broadly ellipsoid. 13. *P. disciformum*.  
(Fig. 3a.)
  - Aeciospores small,  $16-23 \times 20-27 \mu$ .
  - Aeciospores sparsely and strongly verrucose-echinulate. 14. *P. Rosae-arkansanae*.  
(Fig. 12a.)
  - Aeciospores moderately and finely verrucose. 15. *P. americanum*.
  - Aeciospore-wall thick,  $2-3 \mu$ .
  - Infection not causing marked distortion of host.
  - Paraphyses few or none. 16. *P. Rosae-pimpinellifoliae*.  
(Fig. 4a.)
  - Paraphyses abundant and conspicuous.
    - Aeciospores  $21-26 \mu$  long. 17. *P. montivagum*.
    - Aeciospores  $24-30 \mu$  long. 18. *P. Rosae-acicularis*.  
(Fig. 5a.)  - Infection causing distortion; systemic. 19. *P. Rosae-californicae*.  
(Fig. 6a.)

#### KEY TO THE SPECIES OF PHRAGMIDIUM BASED ON TELIOSPORE CHARACTERS

On the tribe Potentilleae.

Teliospore pedicels hygroscopic; § *Euphragmidium*.

Teliospores 3- to 5-celled.

1. *P. Andersoni*.  
(Fig. 10.)

Teliospores 5- to 9-celled. 2. *P. Jonesii.*

(Fig. 1.)

Teliospore pedicels non-hygroscopic; § *Earlea.*

Teliospore-wall chocolate-brown.

Teliospores smooth, 3- to 5-celled. 3. *P. Potentillae.*

(Fig. 9.)

Teliospores verrucose at apex, 2- to 4-celled.

4. *P. Ivesiae.*

(Fig. 7.)

Teliospores light chestnut-brown.

Teliospores coarsely verrucose, 2-celled.

5. *P. bilobulare.*

(Fig. 8.)

Teliospores finely verrucose, 2-celled. 6. *P. Horkeliae.*

(Fig. 11.)

On the tribe Rubeae.

Teliospore pedicels hygroscopic; § *Euphragmidium.*

7. *P. Peckianum.*

Teliospores 4- to 6-celled.

Teliospores 6- to 10-celled.

Teliospore pedicels once the spore length.

8. *P. occidentale.*

Teliospore pedicels once and one-half the spore length.

Teliospores 26-30 × 80-120  $\mu$ . 9. *P. Rubi-idaei.*

(Fig. 2.)

Teliospores 29-34 × 80-110  $\mu$ . 10. *P. Rubi-odorati.*

Teliospore pedicels non-hygroscopic; § *Earlea.* 11. *P. alaskanum.*

On the tribe Roseae.

Teliospore pedicels hygroscopic; § *Euphragmidium.*

Teliospore pedicel swelling abruptly to broadly clavate or globose.

Apiculus long, 7-13  $\mu$ . 12. *P. disciflorum.*

(Fig. 3.)

Apiculus short, 1-5  $\mu$ . 13. *P. Rosae-arkansanae.*

(Fig. 12.)

Teliospore pedicel swelling gradually to lanceolate.

Teliospore-wall chestnut-brown. 14. *P. Rosae-pimpinellifoliae.*

(Fig. 4.)

Teliospore-wall dark chocolate-brown.

Teliospores rounded above.

Teliospores 64-95  $\mu$  long. 15. *P. montivagum.*

Teliospores 64-125  $\mu$  long. 16. *P. americanum.*

Teliospores narrowed above.

Teliospores 48-93  $\mu$  long. 17. *P. Rosae-acicularis.*

(Fig. 5.)

Teliospores 90-130  $\mu$  long. 18. *P. Rosae-californicae.*

(Fig. 6.)

Teliospore pedicel non-hygroscopic; § *Earlea.* 19. *P. speciosum.*

## SUMMARY

1. Segregation of the nineteen North American species of *Phragmidium* based on the character of the teliospore pedicel gives two sections, *Earlea*, including the six species whose pedicels are non-hygroscopic, and *Euphragmidium*, which includes the thirteen species with hygroscopic pedicels.

2. The species are arranged according to three tribes of the host-family Rosaceae, six species occurring on Potentilleae, five on Rubeae, and eight on Roseae.

3. The shape and size of the teliospores, the length and shape of the pedicels, the color and degree of marking of the wall, and the presence or absence of an apiculus are used as differential characters of the individual species within the sections *Earlea* and *Euphragmidium* on each of the three host tribes.

4. On the basis of aeciospore marking the species are discussed under two types as follows: five species have aeciospores which are verrucose with irregular warts and twelve species have aeciospores which are verrucose with regular papillae. In addition one species has strongly echinulate aeciospores, and in one species aecia are unknown.

5. The presence or absence of the aecial paraphyses and their characters are pointed out where characteristic of species.

6. The value of aeciospore size, shape, and wall thickness in the determination of species is discussed and the advantage of using both aeciospore and teliospore characters is emphasized.

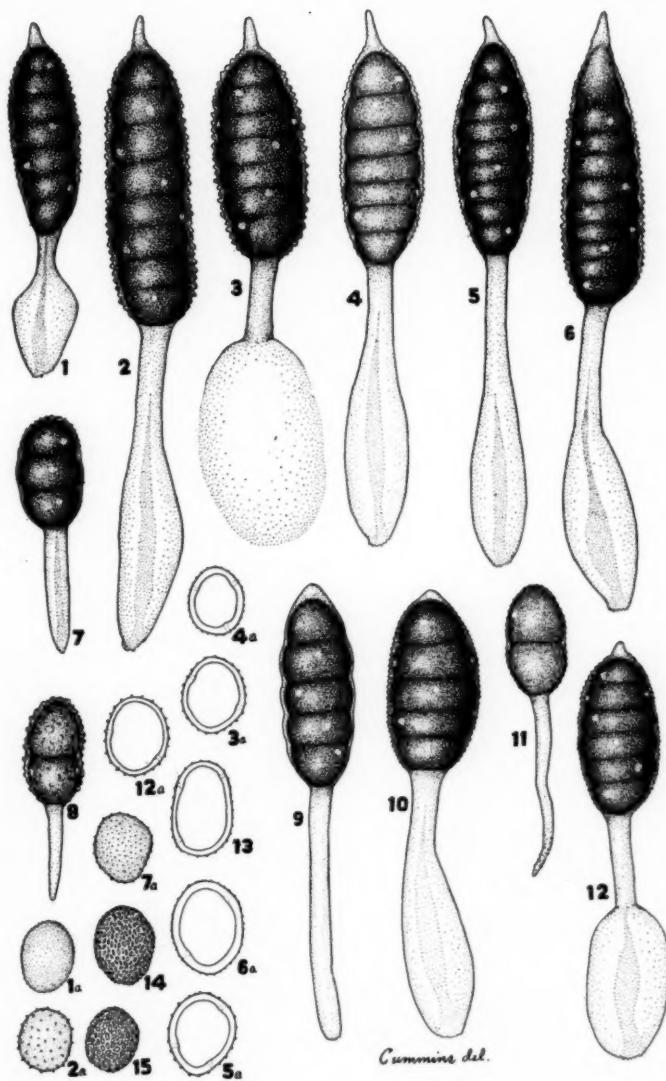
7. The effect of different host species on teliospore morphology is shown in certain species.

8. Keys to the North American species of *Phragmidium*, based on aecial characters and teliospore characters, are included.

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## PHRAGMIDIUM

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#### EXPLANATION OF PLATE 32<sup>1</sup>

##### SPECIES OF PHRAGMIDIUM

Fig. 1, *P. Jonesii*, teliospore showing short fan-shape pedicel; 1a, *P. Jonesii*, aeciospore showing very finely verrucose wall; 2, *P. Rubi-idaei*, showing large cylindric teliospore and long pedicel; 2a, *P. Rubi-idaei*, aeciospore showing strongly echinulate wall; 3, *P. disciflorum*, teliospore showing evanescent lower half of pedicel; 3a, *P. disciflorum*, optical section of an aeciospore showing thin wall; 4, *P. Rosae-pimpinellifoliae*, teliospore showing chestnut-brown wall; 4a, *P. Rosae-pimpinellifoliae*, optical section of an aeciospore showing thick wall; 5, *P. Rosae-acicularis*, showing spindle-shaped teliospore; 5a, *P. Rosae-acicularis*, optical section of an aeciospore showing thick wall; 6, *P. Rosae-californicae*, teliospore showing acuminate apex; 6a, *P. Rosae-californicae*, optical section of large thick-walled aeciospore; 7, *P. Ivesiae*, teliospore showing pedicel and verrucose spore apex; 7a, *P. Ivesiae*, aeciospore showing degrees of marking; 8, *P. biloculare*, teliospore showing evenly verrucose, chestnut-brown wall; 9, *P. Potentillae*, teliospore showing pedicel and smooth spore wall; 10, *P. Andersoni*, showing ellipsoid, non-apiculate teliospore; 11, *P. Horkelliae*, teliospore showing very finely-verrucose, chestnut-brown wall; 12, *P. Rosae-arkansanae*, teliospore showing short apiculus and broadly clavate pedicel; 12a, *P. Rosae-arkansanae*, optical section of an aeciospore showing thin, verrucose-echinulate wall; 13, *P. speciosum*, optical section of large, oblong aeciospore; 14, *P. Peckianum*, showing aeciospore moderately verrucose with irregular warts; 15, *P. Rubi-odorati*, showing aeciospore coarsely verrucose with irregular warts.

<sup>1</sup> All figures were made with the aid of a camera lucida and represent an enlargement of 420 diameters.

## A FURTHER STUDY OF THE MORPHOLOGY AND LIFE HISTORY OF THE ROSE BLACK SPOT FUNGUS

B. O. DODGE

(WITH PLATES 33-35)

One who attempts to grow hybrid roses in this part of the country is apt to find sooner or later some of them being defoliated by the black spot fungus, *Diplocarpon Rosae*. For example, at The New York Botanical Garden it has been observed for several years that certain varieties among our most beautiful roses such as Los Angeles, Mrs. Henry Bowles, Felicity and Padre, always show some spotting in spite of the fungicides which have been applied rather frequently. On the other hand, there are those roses like Red Radiance, Ethel Sommerset, Mrs. C. W. Edwards, La France, Radiance and others, which under the same treatment scarcely ever show black spot. The writer has been asked frequently why it is that the Red Radiance, for example, is comparatively resistant to this parasite. Is it because, as some say, the leaves probably have a cuticle which the fungus cannot penetrate? Or is it due to something more fundamental and inherent in the cytoplasm so that the fungus is unable to live even though it may readily penetrate the cuticle and so cause only a mere flecking. This is among the problems being studied, and some information on this question obtained as a result of preliminary experiments is also presented at this time.

### ARTIFICIAL INFECTION OF RED RADIANCE

Infection work was done in a greenhouse which is held in a rather dry condition. Although a number of potted roses of different varieties have been grown in this house for several years, black spot has seldom developed naturally. The amount of black spot, or the apparent resistance of a rose, evidently depends somewhat on the locality, and also on other conditions

which are apt to vary from year to year, so that a variety that does not happen to show spotting one year may be badly infected the next. Red Radiance was chosen to work with because of its general reputation as a fairly resistant variety. As a check or control Felicity was selected, as it has always shown black spot in our rose garden. The infection chamber employed is the familiar "iceless refrigerator" described by Hunt (4).

In order to learn whether the apparent resistance of Red Radiance is due primarily to the inability of the fungus to penetrate the cuticle of the host, inoculation of leaves was made by wounding them with a needle and then applying spore suspensions at the point of wounding. The leaves of the control Felicity plants were treated in the same manner. The inoculated plants were then left in cool damp chambers for at least two days and then removed to the bench. Ten days to two weeks later black spot began to appear on several leaves of both varieties at the points where they had been inoculated by wounding. This suggested, of course, that here was a type of resistance due to the nature of the cuticle and perhaps also of the cuticularized layers of the outer wall of the epidermal cell. It had been noted in the field that usually the brown or black discoloration of the leaf is, for some time at least, confined to the upper tissues, and in such cases the sori are to be found only on the upper side. Occasionally, however, one finds directly below the spot a small brown discoloration on the lower side showing a few small sori. This indicates that sometimes infection may occur naturally on the lower side of the leaf. After the fungus has gained entrance the mycelium could pass up through the mesophyll tissues and upper epidermis to spread out underneath the cuticle where sori would naturally develop. No one has described detailed experiments to prove that *Diplocarpon*, given an opportunity, does not sometimes gain entrance to the host through the stomatal openings which occur only in the lower epidermis. With this possibility in mind, areas on the lower epidermis of leaves of Felicity and Red Radiance were marked off with India ink and a drop of water containing spores was placed on each area. This was done with many leaves repeatedly and always with the same resulting high percentage of

infection in case of Red Radiance and Felicity, as well as other varieties which have since been tested. In no case, however, did sections of the area exposed to infection show hyphae penetrating the stomatal opening, although, as will be noted later, it very frequently happens that hyphal branches pass between the guard cells and their supporting cells.

While this work was being done, check experiments were made by placing drops of water containing spores on marked areas on the upper epidermis. In certain experiments the surface of the leaves was rubbed with the fingers so that a film of moisture would more readily adhere to the areas inoculated. Whenever fairly young leaves were chosen for the experiments, black spot developed on the Red Radiance just as frequently as it did on Felicity, proving conclusively that under the conditions maintained in these experiments Red Radiance can be artificially infected with black spot just about as easily as can Felicity, Padre, Mrs. Henry Bowles, Charles K. Douglas and other varieties tested. Rubbing the surface of the leaf is not at all necessary, as long as the drop of water containing the spores adheres to the leaf.

These experiments are, of course, far from a test of relative susceptibilities because the dosage in each case was large, and furthermore the number of individual penetrations per spot was not considered at all. Neither was the time during which the inoculated plants were kept in the damp chamber taken into account, except that it was planned to maintain conditions which would be most favorable for infection.

#### HOST-PARASITE RELATIONS

Wolf (7) has worked on the life history of this fungus and has shown that the black discoloration is due to the disorganization of the cells of the leaf and not to the mycelium of the fungus which is said to be practically colorless. He states that the fungus penetrates the cuticle of the upper epidermis, after which the hyphae run along in parallel strands, sending down here and there branches not only between the epidermal and palisade cells but also directly through them, so that the hyphae are intracellular as well as intercellular. As the sorus develops,

the host cells beneath become more or less disorganized, and the mycelium branches and develops abundantly in this region. Wolf's figures show hyphae penetrating the epidermal cells and also the palisade cells.

Our sections of infected leaves, some cut vertical to the leaf surface, others parallel to it (PLATE 33, FIGS. 5-7) show that, as stated by Wolf, the hyphae, soon after the spore germinates, grow in such a way that the branches run along parallel and close together, so that we soon have a layer of fungus tissue mostly one cell thick and made up of several parallel hyphae, which grow along directly beneath the cuticle.

Each hyphal cell has a single large nucleus with a distinct nucleole. Sections cut parallel to the surface of an infected leaf which have been fixed in Flemming's medium, stain readily so that the cytological details show beautifully. A terminal cell about to branch enlarges at the outer end where the nucleus comes to lie. In some cases observed two branches may form about the same time more or less dichotomously, although such a system of branching is not general here. Nuclear division occurs, each branch receiving one nucleus, after which walls cut off the branches from the parent cell. The two branches, at first widely diverging, immediately converge and become tightly pressed together and then continue growing on parallel, each hypha branching again independently. Some of the new branches join the others to broaden the fascicle, while others start off at broad oblique angles to develop a new subcuticular strand. One fascicle may cross another by dipping under it temporarily, coming back to the old level again after the passage is completed. While there is a general appearance of a hyphal system radiating from the points of infection (PLATE 33, FIG. 7), there are all sorts of criss-cross breaks so that a complex net-work is the final outcome (PLATE 34, FIG. 14).

#### HAUSTORIA

As for the subcuticular mycelium and the organization of the acervulus, the work of Wolf (7) has been confirmed. He says, however: "The internal mycelium penetrates the mesophyll of the leaf and furnishes nutriment for the subcuticular part. It

is connected with the latter by occasional hyphae which penetrate the epidermal cells or pass between them." Of the stroma of the acervulus he says: "It is connected with the internal mycelium below by hyphae which extend either through or between the epidermal cells into the mesophyll."

Sections of material fixed from two days up to two months, or even more in case of overwintered leaves, after inoculation, fail to show that mycelial hyphae actually pass through either the epidermal cells or the palisade cells below them. Figure 5 in plate 33 is from a photograph of a surface section at one focus, and figure 6 is of the same area at a slightly lower focus. At A in figure 5 are shown what look to be hyphae growing right through epidermal cells. These are in reality peculiar short hyphal branches growing across the top of these cells imbedded in the cuticularized layers of the outer walls. They are probably haustorium "mother cells." Their haustoria, as well as other haustoria, can be located in figure 6. Figures 7 and 8 are of the same general area but less highly magnified. It is clear from these pictures that we are dealing with typical haustoria and not with intracellular hyphae.

When one notes the very irregular outlines of epidermal cells with their re-entrant angles, it is not strange that one, viewing a section like that shown in figure 4 of plate 33, might be misled as to the nature of the hyphae which appear to be running right through the epidermal cell, when they are in reality intercellular. Figure 3, a photograph of the same section focused to take in the central plane, shows no internal hyphae. On the other hand, intercellular hyphae are very abundant (PLATE 34, FIG. 8), often completely enclosing an epidermal cell on all sides. In material three or four days old the haustoria are well developed in epidermal cells and numerous wherever hyphae are to be found. Figures 1 to 11 in plate 34 show various types of haustoria. Rather long narrow haustoria develop in palisade cells usually starting from the upper wall and extending straight down the cell. For example, three adjacent palisade cells (PLATE 34, FIG. 4) showed one such haustorium in each cell. They can scarcely be made out in this figure, however. Occasionally one finds a haustorium arising from a cell which appears to lie, if

not actually within the host cell cavity, at least not midway between two adjacent walls. Following such fungus cells by changing the focus usually proves that the hypha is, in fact, intercellular and only dips in deeper or splits the wall of the host cell about to be invaded by the haustorium.

The haustoria of *Diplocarpon* are of various forms and sizes, usually containing a single nucleus. The cytological details will be given in another paper. It may be said, however, that as compared with the haustoria of several species of the Asterineae described by Arnaud (1) and others, and with those of *Puccinia Sorghi* studied by Rice (5), there are no peculiarities that set them apart as wholly different. There is usually a bulge of the wall of the host cell at the point of penetration, a fine tube is sent through and a large cup-shaped stalk, probably composed of cellulose, is formed (PLATE 34, FIGS. 6, 7, 9, 10, 11). The haustorium proper penetrates this stalk increasing to its normal diameter just before it emerges. A distinct sheath is frequently visible (PLATE 34, FIGS. 4, 10). The nucleus is usually located at about the center of the haustorium (PLATE 34, FIG. 6). Some haustoria are long and hypha-like (PLATE 34, FIG. 1), while others are rather small showing little of the thickened cup-like base. A single host cell may contain six or eight haustoria, and occasionally one branches so that two or three seem to arise from the same mother-cell enlargement (PLATE 33, FIG. 5).

No evidence has been found to indicate any particular attraction or repulsion as to the relation of haustorium and host nucleus. Chloroplasts persist for some time in an invaded palisade cell.

Directly beneath an old acervulus there is some disorganization of the palisade, but in our material there is not the extensive breaking down of the palisade mesophyll noted by Wolf. Where leaves are allowed to winter over it is difficult to say whether the fungus cells one sees clearly within the epidermal cells are enlarged and perhaps dead haustoria, or whether hyphae may not actually penetrate dead host cells as saprophytic growth working decay. Later on in the spring when the fungus enters upon the development of the new structures about to be described, there is some crushing and destruction of old host cells which are replaced by fungus tissue.

When a leaf is infected through the lower epidermis the first hyphae run along under the cuticle, sending haustoria up into the epidermal cells, and hyphal branches push in between them. So loose is the spongy parenchyma in this region that the individual hyphae may occasionally be seen striking out across the open spaces. Where such hyphae do touch a cell there is apt to be a sort of appressorium developed which stains more deeply. No haustoria have been seen in cells of the spongy parenchyma, though they may no doubt be frequently present.

#### SPERMOGONIA

Higgins (3) in his very interesting studies of life histories of various ascomycetes has frequently noted the development of spermogonia so closely associated with infected areas as to indicate their genetic relationship to the species in question. No one has mentioned such structures in connection with the development of *Diplocarpon* on rose leaves. It may be of interest, therefore, to describe briefly fructifications which were frequently found during the month of March on the black spots of rose leaves which had been left out-doors over winter. Soon after these leaves are brought into the laboratory and placed in moist chambers small blister-like structures usually develop on some of the leaves at various points covered by the black spot fungus. Mounts will show that quantities of very small spermatium-like bodies are being formed from each of the cells of two-celled stalks. At first these stalks, because they were easily loosened from the points of their attachment, and because they resemble the conidia of *Diplocarpon*, were mistaken for ordinary conidia which were budding off microspores. The upper cell, however, instead of being the larger one, which is more often the case with the true conidia, is rather pointed or tapering (PLATE 34, FIG. 12). Furthermore, one would not infrequently find true conidia being developed in the same pustule, but independent of the growth of the microspores (PLATE 34, FIG. 13), in which case it was clear that we had true microconidia or spermatia as contrasted with normal two-celled conidia. No extensive germination studies have been made, but in the few attempts which were made to germinate the small bodies, no growth was seen during the week's

time they were closely observed. Under the same conditions the conidia germinated readily. Some of the pustules were wholly spermatial, others were wholly conidial, and still others were decidedly mixed.

Spermogonia or microconidia of *Phyllostictina (Phoma) carpogena* are not infrequently found on rotting dewberries (2). Sections show that such structures may sometimes contain in addition to masses of spermatia, a few typical pycnospores. This should not be considered strange since spermogonia and pycnidia arise from the same gametophytic mycelium.

Stained sections of spermogonia on black spot of rose leaves show that the spermatia and the cells of their stalks are uninucleate, as are the cells of conidia. One finds in a young spermogonium a palisade layer of large spermatiophores thrusting the cuticle upward. Once space has been provided, spermatia first develop at the tip end of the stalk, and later on buds grow out from the lower cell at the septum. In old spermogonia the stalks are much reduced in size and one finds the spermatia formed as buds on mere knobs of growth. Whether one calls these little bodies spermatia or microconidia is immaterial until their function is ascertained. That they belong in the life history of *Diplocarpon* seems probable for the following reasons. They were found on infected leaves only on the black spots. They arise from a stroma of thick-walled dark-colored cells closely associated with the characteristic parallel hyphal filaments of *Diplocarpon*. They are like true acervuli in being subcuticular. The spermatiophores simulate the two-celled conidia of this fungus. True conidia which germinate readily are often found in unbroken spermogonia during the month of March. Cells of the spermogonial stroma, spermatiophores and spermatia are uninucleate. Furthermore, in view of the work of Higgins on various ascomycetes and of Wolf on *Diplocarpon*, and the facts presented below, the discovery of such additional fruiting structures of this fungus might well be expected.

#### ASCOCARPS AND SUBEPIDERMAL ACERVULI

Wolf (7) has given us a clear description of the development and morphology of the ascocarpic stage which he described as

the type of his new genus *Diplocarpon*. He believed that it must be mainly through this stage that the fungus lives through the winter because he was unable to find acervuli on infected old leaves in the spring. It has since become known, however, that the fungus frequently infects the canes and thus survives the winter and produces conidia the next season. Infection experiments carried out in the greenhouse during the past winter prove that one can usually infect roses by spraying them with water in which old infected rose leaves have been soaked for a few minutes. As noted previously, if these old leaves are brought into the laboratory in March and kept a few days in a moist chamber subcuticular acervuli may develop from the thick-walled dark-brown mycelial strands. These conidia germinate readily. The ascocarpic stage, then, in the climate of New York City is not essential for the spread of the fungus to the new spring growth.

At the close of the growing season of 1929 infected leaves were enclosed in a wire cage and then stored under shrubbery throughout the winter. Many of these old leaves were examined during the month of April but no ascocarps were found. The experiment was repeated in 1930. The leaves were carefully examined several times during March and April, 1931. If ascocarps were present they were not discovered. After each inspection the leaves were again exposed to the weather.

Wolf says that at Ithaca, N. Y., ascocarps begin to form sometime early in April and reach full maturity during that month. His developmental stages were obtained by fixing material at intervals during April. The circular perithecial shield is formed from radiating strands of thick-walled brown cells just beneath the cuticle. The fertile stroma develops between the epidermis and the palisade parenchyma. The central cells of the stroma are thin-walled and have stainable contents. It is from the basal portion of this tissue that paraphyses and asci are developed. The ascospores are two-celled and further resemble the conidia closely in color, size and shape, except that the ascospores are not so strongly constricted at the septum. They are discharged as the perithecium breaks open, and pile up in a whitish mass.

The production of ascocarps by a fungus is well known to be a matter of much uncertainty even in nature, depending on many factors not at all understood as yet. Evidently the difference between the cold winters of Ithaca with much snow, and the mild winters which have prevailed at New York City during the past few years could well account for the absence of ascocarps on our material. It is interesting, nevertheless, to find in our sections of infected spots on the old leaves fixed at intervals during March and April, structures (PLATE 35, FIGS. 4-7) which correspond very closely in their origin and mode of development with the ascocarps described by Wolf. The main difference being that in his structures paraphyses are formed and asci with ascospores are developed, while in ours the upward growing short filaments cut off conidia. Wolf's figures 6 to 10 of the early stages in the formation of the subepidermal ascocarps represent very well corresponding stages in the development of our internal fruit bodies. The latter have no definitely organized walls, still one might prefer to call them pycnidia. The same subcuticular crust of thick-walled cells covers the top like a shield in both cases. The radiating pattern of the shield elements is not striking however. The same massing of subepidermal stromatic tissue is found. The outer cells of the stroma are likewise thick-walled and carbonized, the inner ones are thin-walled and have stainable contents. Space is provided in the same way by crushing and raising the epidermis and thrusting aside the palisade tissue. The initial central filaments which develop within this stroma furthermore resemble the paraphyses with their thickened top ends figured by Wolf. They push up into the fungus tissue and remains of epidermal cells above. Here the exact duplication of structures in the various stages of development suffers a break in method or principle and yet the end products, ascospores and conidia respectively, are exactly alike and are discharged in similar whitish masses.

Authors have at various times described ascocarps which were said to have appropriated pycnidia or other asexual fructifications to their own use, asci, for example, appearing in the cavity, the basal sporogenous tissue of which had previously produced conidia. Such forehandedness has not been proved against

*Diplocarpon* as yet however. Only conidia have been found in the subepidermal fruit bodies on old leaves wintered over in the park at New York City.

The first conidia are cut off at the ends of rather thick filaments which are three or four cells long. A slight constriction occurs at the second septum and the upper portion is freed as a two-celled conidium. The remaining portion evidently can elongate and produce another spore, or become a spore in turn. Sections of a fruit body fixed after it had discharged a mass of spores (PLATE 35, FIG. 4) show very few filaments of the sort that initiate spore formation. The spores instead either have a one-celled stalk or arise directly from thin-walled sporogenous cells of the stroma. Crushed mounts of old material also show that two or three spores may arise at the same time from such cells and not have individual stalks as do the first spores to appear. The formation of a central cavity is mostly brought about through the upward thrust of these conidiophores, although some of the pressure is likely due to the partial disorganization and swelling, not only of a few of the thin-walled cells at the center, but also of some of the first formed spores. It enlarges just to the extent that the more deeply lying sporogenous cells take the place of those consumed in spore production.

The organization of the asexual fruit body of *Phoma (Phyllostictina) carpogena* (2) which is called a pycnidium is much the same. Why not call these deep-seated organs of *Diplocarpon* pycnidia instead of acervuli? The presence of a true ostiolar growth in one and not the other is immaterial. The *Phoma* has a more definite stroma the size of which is fixed before spore formation begins. In our old material the stroma above breaks away and exposes the sporogenous tissue (PLATE 35, FIG. 4) somewhat as is the case with the ordinary acervulus. Wolf refers to species of *Marssonnia* as having subepidermal acervuli. For the present at least we shall also refer to the deep-seated fruit bodies of *Diplocarpon* as subepidermal acervuli and to the normal summer type as subcuticular acervuli.

The conidia are discharged in a whitish mass as the acervulus breaks open. Wolf was unable to germinate the ascospores which he found heaped up in whitish masses, unless he placed

them in a drop of water on a rose leaf. The conidia formed in the subepidermal acervuli just described, on the contrary, germinate readily on an agar medium. Nevertheless we have here another striking parallelism not only in the method of the origin and development of the ascocarps and the subepidermal acervuli, but also in the color, form, size and type of germination of their ascospores and conidia respectively. This is plainly seen when one compares Wolf's figures of ascocarps and ascospores with our figures of the subepidermal acervuli and their conidia (PLATE 35). The strong resemblances between the ascocarps and the pycnidium of *Schizophyllum stramineum* (2) afford another beautiful illustration of such a parallelism.

That the subepidermal fruit bodies described above belong in the life history of *Diplocarpon* has been proved by inoculation experiments using cultures from single spores, so that there is no question in this regard. On the sixth day after inoculating the leaves, brown spots bearing typical subcuticular sori began to appear. At the end of the second week some eighty or more such spots had developed at points where drops of spore suspension had been placed. No spots developed on other leaves of these plants. The conidia which develop in these new sori are the same size and shape as are those shown in figure 1, plate 3, which were taken from a subepidermal fruit body. Conidia from cultures obtained from single spores from such sori are of this same type also. Regardless of the source of conidia they all germinate in the same characteristic fashion. The first germ tube is put out from a spot near the center of the upper, larger cell, and as it elongates, grows up into the air. The other cell then germinates and other germ tubes develop from the tip ends of both cells of the spore.

The conidia from an ordinary subcuticular acervulus shown in figure 2 seem to be more constricted at the septum. This may indicate a slight strain difference which can be followed out later by further inoculation experiments. Practically every one of the old leaves stored outside in two different cages developed subepidermal sori when they were finally brought into the laboratory during the last days in April. The main point brought out, in any event, is that when one inoculates a leaf with conidia

from a subepidermal sorus on over-wintered leaves, subcuticular sori are developed.

The tendency to form two-celled structures is manifested in four ways by this fungus. The spermatiophores are rather thick two-celled organs. The subcuticular acervuli develop two-celled hyaline conidia which resemble somewhat the spermatiophores. The subepidermal acervuli also form two-celled conidia which are even more like the two-celled ascospores described by Wolf than they are like conidia from ordinary subcuticular sori (PLATE 35, FIGS. 1 and 2). Furthermore the conidia in any old culture tend to develop very small two-celled secondary conidia.

Shear and Dodge (6) proved by many single spore cultures that *Pezizella Lythri* produces two genotypically different kinds of asexual fruit bodies. The sporodochial *Hainesia* stage develops exactly the same kind of spore as does the thick-walled sclerotium-like *Ptilidium* (*Sclerotiopsis*) pycnidium. The former is more adapted to spread the fungus widely during the summer. The latter stage often develops slowly during the winter and opens in the spring. The subcuticular acervuli of *Diplocarpon* are supplied with nourishment by a parasitic mycelium and provide conidia during the growing season of the host. The deep-seated subepidermal acervuli, on the other hand, are nourished in a purely saprophytic way by mycelium living on the dead host leaves, and provide spores for spring infection of the first rose leaves that appear.

It is encouraging to observe the great change coming about in the minds of botanists in recent years as regards sexual reproduction in the fungi. In view of the positive evidence being adduced that the spermatia of the rusts function in fertilization, there is a tendency to look with more favor on the suggestion of a similar function of the so-called microspores or spermatia of the ascomycetes. Proof that the structures which have developed on over-wintered rose leaves infected with *Diplocarpon*, and which have been called spermogonia in this paper, are connected with *Diplocarpon* is yet to be obtained. The fact that they frequently develop immediately above a subepidermal acervulus, and sometimes also form normal two-celled conidia, is evidence not to be disregarded. One can scarcely refrain from

hoping to find here another case of heterothallism, which would help to explain certain points regarding the formation of ascocarps as yet not clear.

Ascocarps, described by Wolf, but not seen in our material, develop on old leaves in April. They are deep-seated structures arising from a stroma between the epidermis and the palisade layer, and are capped by a shield of thick-walled brown cells which are developed in a radiating pattern from subcuticular hyphal strands above. Filamentous paraphyses with thickened tips first occupy the central cavity, then, by the end of April, asci with colorless two-celled spores appear. The ascospores are  $20-25 \times 5-6 \mu$ , not constricted at the septum. They are extruded in whitish masses as ascocarps break open. The ascospores germinate only in water on rose leaves.

The morphology of the structures described in this paper was worked out from crushed mounts and from stained slides. The writer is greatly indebted to Miss Marjorie Swift who made the stained preparations and who assisted in the experimental work. The cytological details and general discussion will be included in another paper.

#### SUMMARY

A description of the main features to be noted in a study of *Diplocarpon* on rose would include the following. Infection is most noticeable as black spots on the leaves, though the canes of certain varieties are subject to attack. Infection occurs directly through the cuticle on either side of the leaf. The superficial, primary mycelium is subcuticular and is composed of colorless uninucleate cells, the hyphae forming a network and tending to be associated in fascicles composed of several parallel filaments radiating from the point of infection. The internal mycelium is intercellular.

Haustoria, especially conspicuous in epidermal and palisade cells, are simple uninucleate structures, usually with a conspicuous thick cup-shaped stalk and a sheath sometimes fairly distinct. The black spot is due to disorganization of host cells and appears one or two weeks after inoculation.

Summer acervuli, usually on the upper side of the leaf, occa-

sionally on the lower, are subcuticular and contain two-celled colorless conidia arising from short inconspicuous cells of the thin basal stroma. The conidia,  $18-25 \times 5-6 \mu$ , are usually constricted at the septum and germinate readily in water or on agar media.

Spermogonia or microacervuli develop on the black spots on old leaves in March and April. They are subcuticular and usually on the upper side of the leaf. The spermatia are uninucleate,  $2-3 \mu$  long, and resemble very small spores. They are cut off from two-celled stalks simulating the conidia except that they are smaller and taper upward. Sometimes normal two-celled conidia are present in spermogonia.

Internal deep-seated acervuli develop on old leaves early in April in a stroma located between the upper epidermis and the palisade layer. They are capped by a mass of thick-walled brown cells. They may rarely develop in the spongy parenchyma on the lower side of the leaf. The first conidiophores are filamentous and usually three or four cells long, the upper two cells being cut off as a true two-celled conidium. In old fruit bodies the conidia have a single stalk cell or arise directly from the sporogenous tissue cells, two or three spores often arising from the same cell, without having individual stalks. The conidia are colorless,  $20-25 \times 5-6 \mu$ , the upper cell usually thicker, not constricted noticeably at the septum. They are extruded in a whitish mass as the fruit body breaks open. The conidia germinate readily in water or on agar media.

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#### EXPLANATION OF PLATES

*Diplocarpon Rosae*

##### PLATE 33

Fig. 1. Section of old rose leaf showing subcuticular spermogonia March 22; Fig. 2. A deep-seated sorus with epidermal cells above much disorganized. Numerous two-celled spores loose in the cavity; Figs. 3, 4. Two views of the same section of a subcuticular acervulus at slightly different focuses to show that hyphae which appear to pass directly down through this epidermal cell are in reality running down between two adjacent cells; Fig. 5. Section of the upper epidermis cut parallel to the leaf surface. At A two haustorium mother-cells embedded in the upper wall of the epidermal cells; characteristic parallel strands of hyphae; Fig. 6. Same area at a slightly lower focus to show three or four haustoria in each cell directly beneath the fascicles of subcuticular surface hyphae shown in Fig. 5; Figs. 7, 8. Two views of the same general region as the preceding less highly magnified, fig. 8 at a lower focus. No haustoria in the light colored cells in the region where fig. 7 shows no subcuticular hyphae.

##### PLATE 34

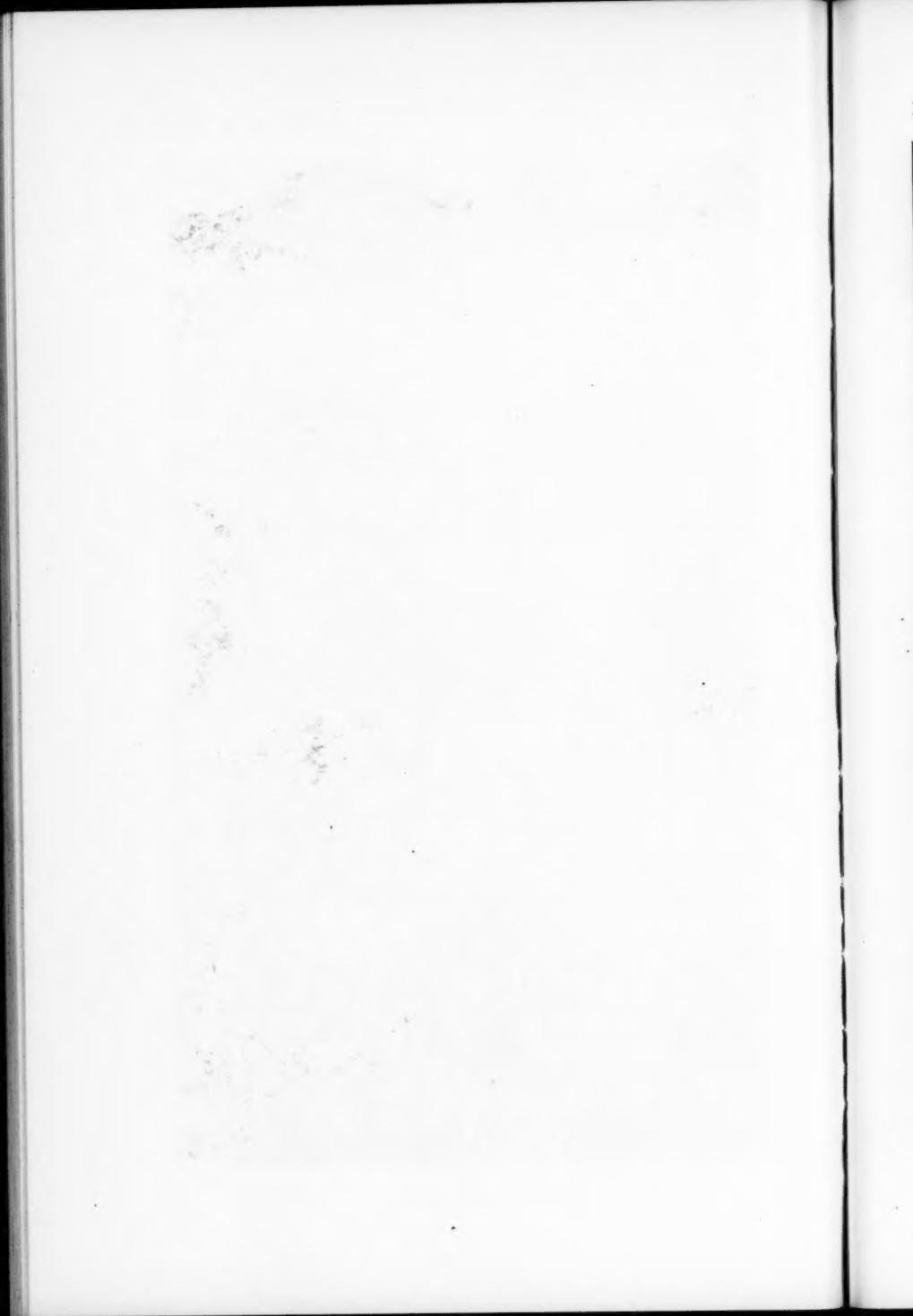
Fig. 1. A large hypha-like haustorium in the cell at the left. A distinct sheath surrounds the haustorium in the cell at the right; Figs. 2, 3. Two views of the same host cells at different focuses. Cut ends of intercellular hyphae from which haustoria with large cup-shaped stalks arise are also visible. At the left in fig. 3 a cross section view of the cut end of haustorium stalk; Fig. 4. Epidermal cells beneath a young acervulus show sheathed haustoria. Each of three palisade cells also contains a haustorium running directly downward. Such a type might be mistaken for an intracellular hypha. They are not readily made out in this figure although distinct in the preparation; Fig. 5. A long epidermal cell showing eight or ten small haustoria with pouched ends; Figs. 6, 7 and 9. Other typical haustoria in epidermal cells; Fig. 8. From a section cut parallel to the leaf surface. Shows cut ends of many intercellular hyphae which surround these epidermal cells. The haustoria present in some of the cells do not show well in this picture; Fig. 10. The cellulose thickening extends well out around the haustorium; Fig. 11. A large haustorium growing down into a subepidermal cell of the type one sees above veins. The photograph was mounted sidewise; Fig. 12. Shows the subcuticular spermogonial stroma of dark-colored hyphae and two-celled pointed spermatiophores; at the center a small two-celled conidium; Fig. 13. Section of a spermogonium which shows one of the several large two-celled conidia which were mixed in with the spermatia in this structure; Fig. 14. Subcuticular fascicles of hyphae crossing each other.

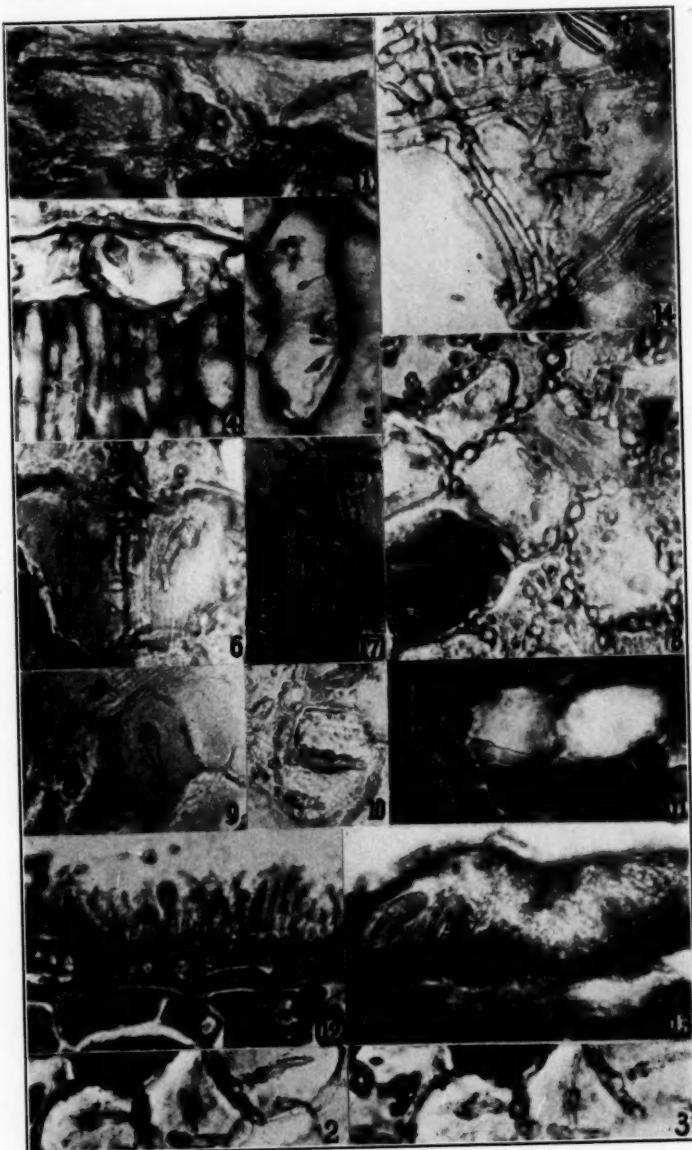
## PLATE 35

Fig. 1. Conidia from a subepidermal fruit body on an old leaf; Fig. 2. Conidia from a subcuticular acervulus of the normal summer type. The same magnification in figs. 1 and 2; Fig. 3. Spermatia massed in a typical subcuticular spermogonium; Fig. 4. Old subepidermal acervulus after discharging its white mass of conidia like those shown in fig. 1; Fig. 5. Young subepidermal fruit body just at the time the central cavity is beginning to be formed; Fig. 6. An older stage showing sporophores developing two-celled conidia. The two black areas above are old epidermal cells surrounded by thick-walled dark-colored fungus cells; Fig. 7. Fruit body nearly mature. Shows some conidia loose in the cavity. The stromatic tissue above is just breaking open. Figs. 5, 6 and 7 have the same magnification. Fig. 4 shows a still older stage and is less highly magnified.

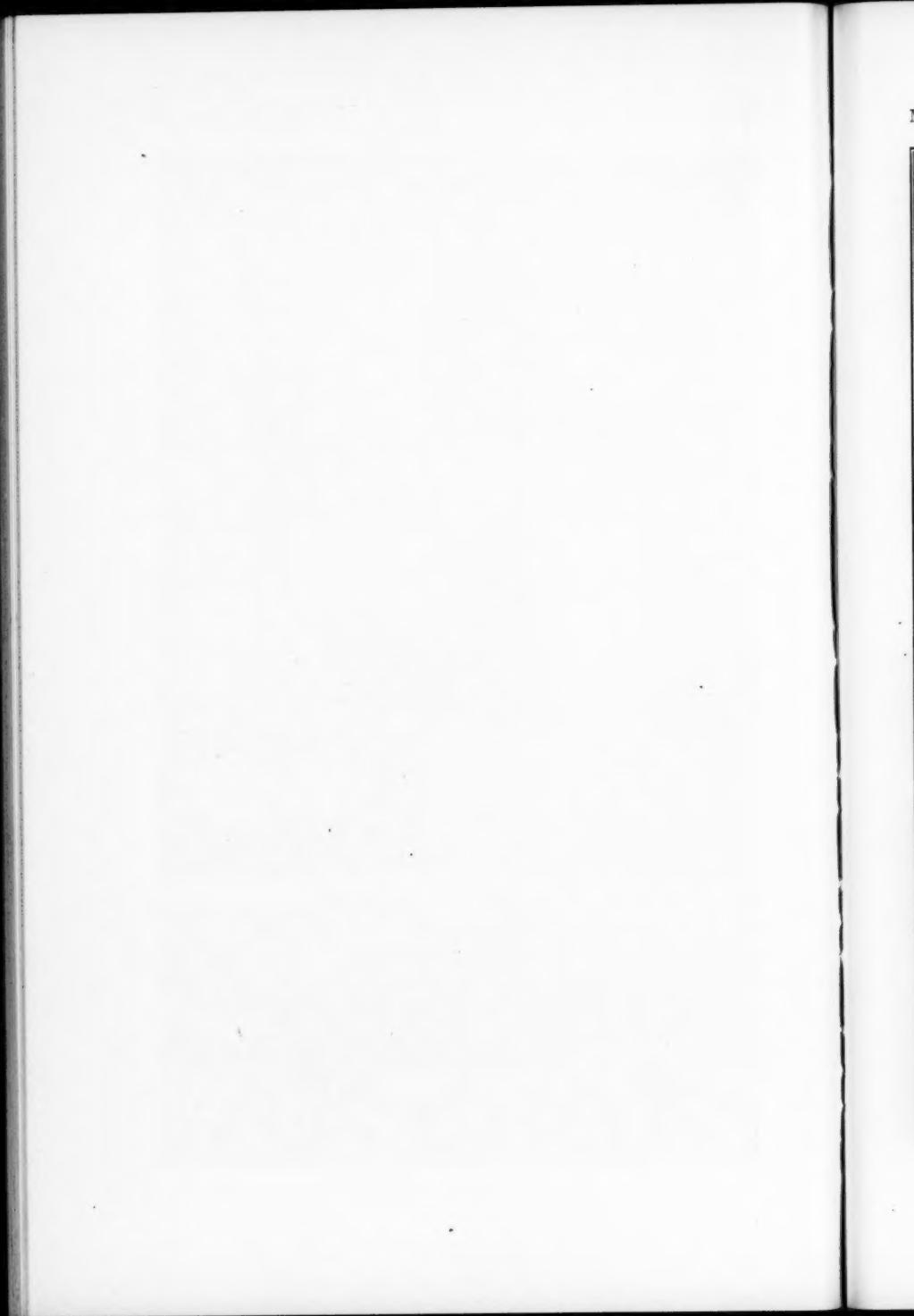


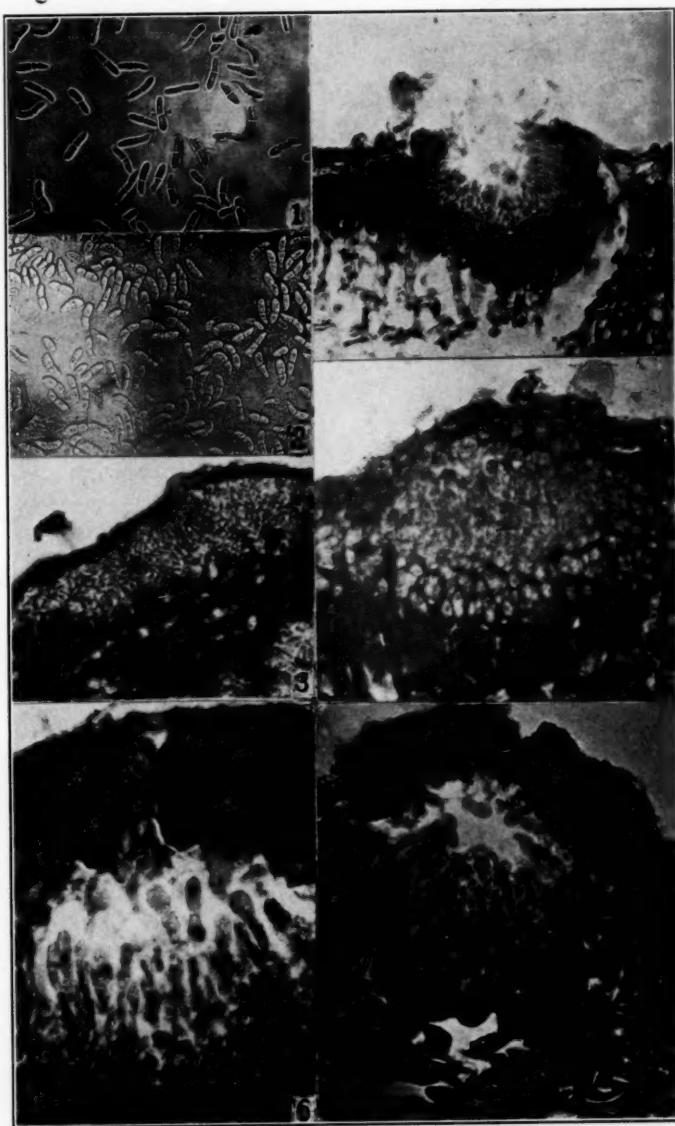
DIPLOCARPON ROSAE



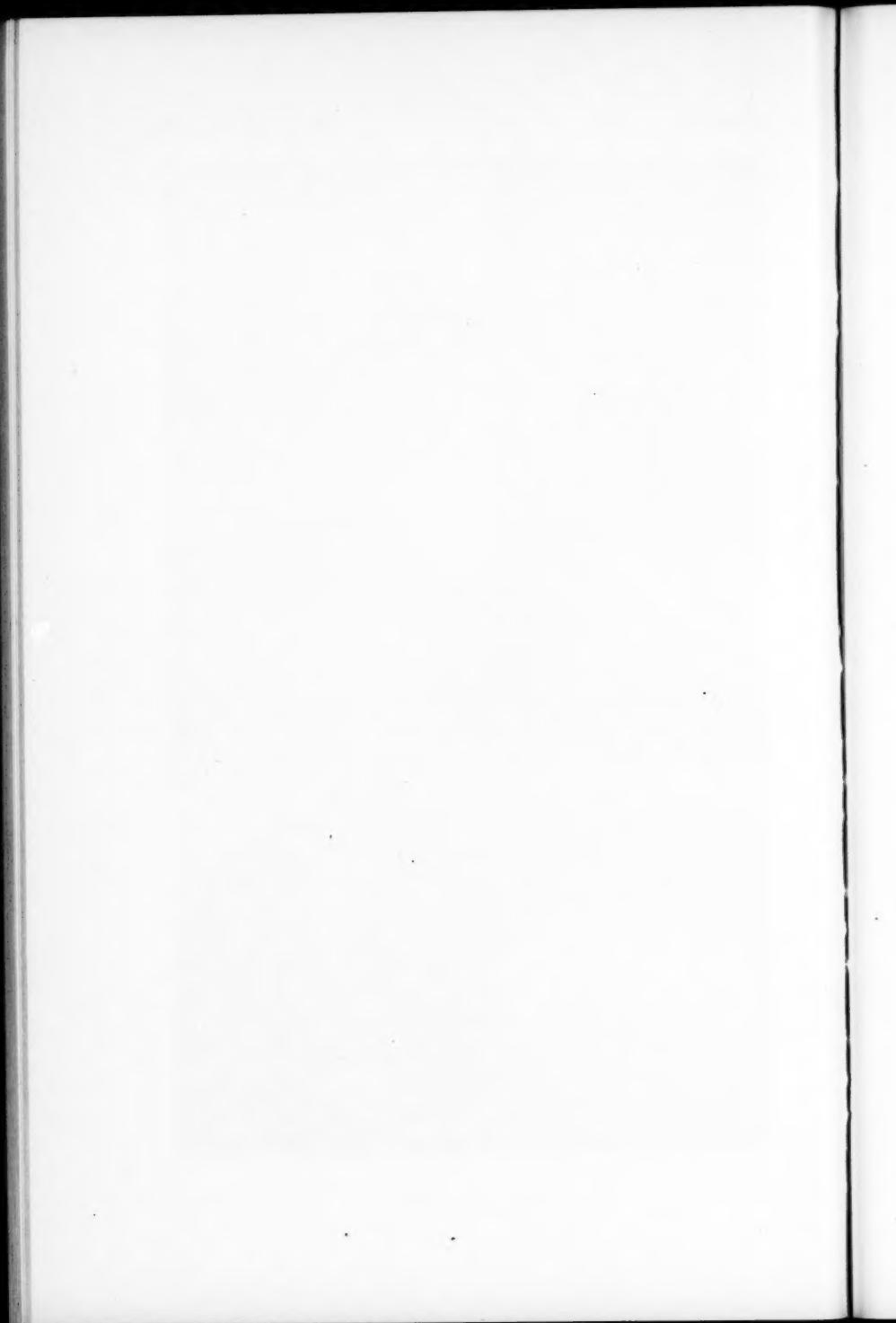


DIPLOCARPON ROSAE





DIPLOCARPON ROSAE



## THE RUSTS OF SOUTH AMERICA BASED ON THE HOLWAY COLLECTIONS—V<sup>1</sup>

H. S. JACKSON

### SPECIES ON EUPHORBIACEAE

168. AECIDIUM HYPSSOPHILUM Speg. Anal. Mus. Nac. Buenos Aires **19**: 321. 1909.

*Euphorbia portulacoides* L. Termas de Chillón, Chile, Dec. 27, 1919, 251.

Holway's field notes indicate that this *Aecidium* is associated with *Uromyces andinus* P. Magn., but in his opinion it has no connection with it. Spegazzini considered this *Aecidium* to be connected with *U. hypsophilus* Speg. Tranzschel and Sydow have independently expressed the opinion that this *Uromyces* is the same as *U. andinus* and Sydow considers the connection doubtful. For these reasons I have listed the collection separately, with the possibility in mind that it is the aecial stage of a heteroecious species, the diplont of which occurs on Fabaceae. On the other hand, it would be interesting to have a study made of the germination of the spores of this *Aecidium*. It may well prove to be an *Endophyllum*.

### **Arthuria** Jackson, gen. nov.

Pycnia subcuticular, other sori subepidermal; aecia caeomoid, aeciospore wall echinulate; uredinia like the aecia, urediniospores catenulate with intercalary cells; telia semi-waxy, teliospores catenulate, thin-walled, germinating at once.

We name this genus in honor of Dr. J. C. Arthur, whose contributions to uredinology are well known. The structure suggests relationship with *Chrysomyxa* except that the aecia are

<sup>1</sup> Joint contribution from the Department of Botany, University of Toronto, and the Department of Botany, Purdue University Agricultural Experiment Station. Prepared with the aid of a grant from the American Association for the Advancement of Science. The fifth of a series of papers bearing the same title (see *MYCOLOGIA* **18**: 139–163. 1926; **19**: 51–65. 1927; **23**: 96–116. 1931; **23**: 332–364. 1931).

caeomoid and the pycnia subcuticular. It differs from *Bubakia* in the catenulate urediniospores.

169. **Arthuria catenulata** Jackson & Holway, sp. nov.

0. Pycnia chiefly epiphyllous, sometimes amphigenous, subcuticular, conspicuous, gregarious in small groups of three to eight, punctiform, flattened-hemisphaeric or occasionally conic, often confluent, 38–50  $\mu$  high by 75–100  $\mu$  broad.

I. Aecia caeomoid, chiefly hypophyllous, occasionally amphigenous, rounded or irregular, 0.3–0.8 mm. across, occurring singly opposite the pycnia or in groups, and then often confluent and circinate about the pycnia, early naked, pulverulent, golden or light cinnamon brown, ruptured epidermis conspicuous; aeciospores catenulate, obovate or ellipsoid, 18–25 by 26–38  $\mu$ ; wall colorless, 2–3  $\mu$  thick, sparsely and prominently echinulate, the pores obscure.

II. Uredinia hypophyllous, like the aecia in appearance and structure, scattered or gregarious, often with a large central sorus surrounded by an encircling group of smaller sori; urediniospores like the aeciospores.

III. Telia hypophyllous, scattered or gregarious, often with a large central sorus 0.6–1 mm. in diameter, surrounded by an encircling group of smaller sori, possibly developing in old uredinia, waxy or semi-waxy, at first golden-brown, becoming whitish on germination; teliospores catenulate, chains composed of 3–8 spores, slightly constricted at the septa, teliospores somewhat barrel shaped, 20–25 by 25–35  $\mu$ , adhering, germinating at once and in succession from apex to base of chain; wall thin, 1–1.5  $\mu$ , colorless, smooth; basidium stout, composed of four cells, basidiospores oblong, 11–13 by 18–20  $\mu$ .

*Croton celtidifolius* Baell. São Paulo, Brazil, Feb. 15, 1922, 1561.

*Croton* sp. Paineiras, Rio de Janeiro, Brazil, Aug. 17, 1921, 1046 (type); Petropolis, Rio de Janeiro, Brazil, Oct. 20, 1921, 1237; Bosque da Saude, São Paulo, Brazil, Jan. 31, 1922, 1518; Campos do Jordão, São Paulo, Brazil, Apr. 23, 1922, 1758.

I have little hesitancy in basing a genus on this interesting species. The combination of characters seems very different from anything previously described. It has not been possible to detect any essential difference between the aecia and uredinia or between the spores of the two stages. Should the uredinia be interpreted as repeating aecia?

It is possible that this may be the same as *Uredo Crotonis* P. Henn. Authentic material has not been available for comparison. In that species, however, the sorus is described as "ferrugino-ochraceis" and the urediniospores as having 4 equatorial pores. We have not been able to detect pores in our species.

The sori all appear to be naked, without peridia or paraphyses. Carefully made sections demonstrate beyond question that the spores in the aecia and uredinia are formed in the same manner, in chains with very evident intercalary cells.

170. *Bubakia argentinensis* (Speg.) Jackson & Holway, comb. nov.

*Uredo crotonicola* P. Henn. *Hedwigia* 35: 251. 1896.

*Melampsora argentinensis* Speg. *Anal. Soc. Cient. Argent.* 47: 266. 1899.

*Schroeteriaster argentinensis* Sydow, *Monog. Ured.* 3: 401. 1914.

*Phakopsora argentinensis* Arth. *Bull. Torrey Club* 44: 508. 1917.

*Croton chaetophorus* Muell. Arg. São Paulo, Feb. 6, 1922, 1538.

*Croton hirtus* L'Hér. Bello Horizonte, Minas Geraes, Brazil, Dec. 4, 1921, 1365.

Two collections showing uredinia only have been included here, one of which is on the same host as the type of *Melampsora argentiensis*. The urediniospores are rather small, usually not exceeding 25  $\mu$  in length. The wall is rather closely and finely echinulate. The species seems to fit the revised uredinial description as given by Sydow (*Monog. Ured.* 4: 578. 1924). The spores are occasionally slightly thickened at the apex, as noted by Sydow. *Uredo crotonicola* P. Henn. is included in the synonymy on the authority of Sydow, who has apparently compared authentic material. Arthur (*Mycologia* 14: 13. 1922) assigned this *Uredo* to *Bubakia* (*Phakopsora*) *Crotonis* (Cooke) Arth. It seems best, however, to assign it to the above species for the present. It is still a possibility that the two species may be identical. More ample material of telia is needed before this question can be settled.

One of the collections listed above (1365) shows pycnia with primary uredinia. These are amphigenous, flattened hemisphaeric, 36–45  $\mu$  high by 65–100  $\mu$  broad, and occur with the primary uredinia on slightly hypertrophied spots. The urediniospores in the primary uredinia appear to be borne on short pedicels. If our identification is correct this is the first record of pycnia for a species of *Bubakia*, and indicates a brachy-type of life history.

171. ***Bubakia Ulei* (Syd.) Jackson & Holway, comb. nov.**

*Uredo Phyllanthi* P. Henn. *Hedwigia* 35: 249. 1896.  
*Schroeteriaster Ulei* Sydow, *Ann. Myc.* 14: 70. 1916.

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*Phyllanthus brasiliensis* (Aubl.) Rusby. Coroico, Nor Yungas, Bolivia, June 11, 1920, 734.

The collection consists of uredinia only but seems to agree with the description given by Sydow, who assigns *Uredo Phyllanthi* P. Henn. as a synonym. Arthur's record of the latter from Trinidad (Thaxter 31) is an error. This specimen is the uredinal stage of a *Ravenelia*, probably *R. appendiculata* Lagerh. & Diet.

172. ***OLIVIA CAPITULIFORMIS* (P. Henn.) Arth. *Mycologia* 9: 61. 1917.**

*Uredo capituliformis* P. Henn. *Hedwigia* 34: 97. 1895.  
*Ravenelia capituliformis* P. Henn. *Hedwigia* 43: 160. 1904.

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*Alchornea Iricurana* Casar. Rio de Janeiro, Brazil, Aug. 29, 1921, II, 1081.

*Alchornea pycnogyne* Muell. Arg. São Paulo, Brazil, Jan. 22, 1922, II, III, 1492.

A characteristic species which was originally described from Goyaz, Brazil. It is also known in the West Indies from Porto Rico and Tortala.

173. ***Puccinia Actinostemonis* Jackson & Holway, sp. nov.**

II. Uredinia amphigenous, scattered or gregarious, often on discolored spots, occasionally locally systemic and then occurring evenly distributed on stems, petioles and leaves, irregularly

circular in outline, 0.5–0.8 mm. across, often confluent, tardily naked, yellowish, pulverulent; ruptured epidermis noticeable; urediniospores broadly ellipsoid or obovoid, 16–18 by 18–23  $\mu$ ; wall colorless, 1.5–2  $\mu$  thick, evenly, closely and finely echinulate; pores obscure.

III. Telia amphigenous, chiefly hypophyllous, gregarious on discolored spots, often confluent, tardily naked, cinnamon brown, compact, ruptured epidermis conspicuous; teliospores clavate or cylindrical, 15–19 by 32–50  $\mu$ , rounded or obtuse above, rounded or narrowed below, slightly or not constricted, germinating at once with 4-celled basidium; wall light cinnamon brown, thin, 1–1.5  $\mu$ , thickened to 2.5–3  $\mu$  at apex, slightly thickened at angles near septum, smooth; pedicel short, colorless.

*Actinostemon* sp. Lapa, São Paulo, Brazil, Feb. 27, 1922,  
1600.

174. **Puccinia festata** Jackson & Holway, sp. nov.

? *Uredo Cornui* Har. Bull. Soc. Myc. Fr. 7: 147. 1891.

II. Uredinia chiefly hypophyllous, scattered, small, round, 0.2–0.5 mm. across, early naked, yellowish, compact, then pulverulent, ruptured epidermis not noticeable; paraphyses apparently chiefly peripheral, clavate or capitate, 60–75  $\mu$  long, the apex 18–25  $\mu$  broad, wall colorless or slightly tinted, uniformly thin, 1  $\mu$  or less; urediniospores broadly ellipsoid, 20–23 by 26–32  $\mu$ , wall colorless, thin, 1.5–2  $\mu$ , closely, evenly and minutely echinulate; the pores obscure.

III. Telia amphigenous, scattered, small, round, 0.2–0.8  $\mu$  across, tardily naked, pulverulent, blackish brown, ruptured epidermis conspicuous; teliospores irregularly ellipsoid, 25–32 by 38–56  $\mu$ , rounded below, rounded above with an abruptly acute umbo; wall chestnut brown, uniformly 2.5–3.5  $\mu$  thick, except at the umbo, evenly, closely, finely but prominently verrucose; pedicel colorless, tinted next to the spore, equaling the spore or shorter.

*Euphorbia*. Quito, Ecuador, Aug. 18, 1920, 912; Cuenca, Prov. del Aguay, Ecuador, Sept. 15, 1920, 990 (type); Huigra, Prov. Chimborazo, Ecuador, Aug. 6, 1920, 852.

The uredinal stage of this species agrees with a specimen collected by Lagerheim at Quito, Ecuador, December, 1899, which is assigned to *Uredo Cornui* Har. No authentic material of this species has been available, and the assignment of that *Uredo* to this species is problematical.

The second specimen listed (990), which is designated the type, consists primarily of uredinia with a few epiphyllous telia. The last collection listed (852) consists primarily of telia, these occur on either side of the leaf near the base. A very few uredinia occur on these leaves, leaving no doubt as to the identity of all the collections. The paraphyses which are abundant in the uredinia appear to be absent in the telia. These would bear a detailed study, as they seem to be borne in fascicles. Because of lack of time and the scanty material available no attempt has been made to work out the details of their formation.

175. *RAVENELIA APPENDICULATA* Lagerh. & Diet.; Dietel, *Hedwigia* 33: 47. 1894.

*Phyllanthus brasiliensis* (Aubl.) Rusby. Villa Aspiazu, Prov. Sur Yungas, Bolivia, May 31, 1920, 689.

Originally described from Ecuador, this species has otherwise been previously reported from South America only from Venezuela. It is also known in Central America from Guatemala and southern Mexico. Both uredinia and telia are present in the collection listed above.

176. *Uredo pavida* Jackson & Holway, sp. nov.

II. Uredinia hypophyllous, scattered, small, round, 0.2–0.4 mm. across, tardily naked, cinnamon brown, pulverulent, ruptured epidermis conspicuous; paraphyses clavate or cylindrical, scattered throughout the sorus, wall colorless, slightly thickened above; urediniospores broadly ellipsoid or obovoid, 16–20 by 26–34  $\mu$ ; wall golden brown, thin, 1–1.5  $\mu$ , in most spores uniformly thick, in a small percentage thickened at apex occasionally to 6  $\mu$ , moderately but sharply echinulate; the pores obscure.

*Croton compressus* Lam. Rio de Janeiro, Brazil, Aug. 29, 1921, 1080; Nov. 13, 1921, 1296; Campo Grande, Rio de Janeiro, Sept. 19, 1921, 1126; Campinas, São Paulo, Brazil, Apr. 3, 1922, 1694.

This *Uredo* is quite different from the one which we have assigned to *Bubakia argentiensis*. The spores are larger and more sharply and somewhat more sparsely echinulate. It does not seem to agree with the description of *Uredo Crotonis* P. Henn. In that species the soral characters are quite different,

the spores are larger, with thicker walls, the wall measurement is given as  $2\frac{1}{2}$ –4  $\mu$  by Sydow and no mention is made of paraphyses.

177. *Uredo Tijucae* Jackson & Holway, sp. nov.

II. Uredinia subcuticular, hypophylloous, on yellowish spots, scattered, small, round, 0.2–0.4 mm. across, early naked, cinnamon brown, pulverulent, ruptured cuticle conspicuous; urediniospores ellipsoid or obovoid, 15–18 by 24–25  $\mu$ ; wall thin, 1–1.5  $\mu$ , cinnamon brown with some tendency to be darker in upper part of spore, finely and closely verrucose; pores 2, equatorial.

*Phyllanthus lathyroides* H.B.K. Tijuca, Rio de Janeiro, Brazil, Aug. 19, 1921, 1056 (type); Petropolis, Rio de Janeiro, Brazil, Oct. 25, 1921, 1245.

It seems probable that this is the uredinal stage of a *Ravenelia*. It differs, however, from any described on this host genus. Paraphyses appear to be absent. Our specimens agree with Ule's collection 2214 from Rio de Janeiro issued as *Uredo Phyllanthi* P. Henn. It is quite different from that species, however, which has larger irregular spores and has been assigned by Sydow to *Schroeteriaster Ulei* Sydow.

178. *Uredo valentula* Jackson & Holway, sp. nov.

0. Pycnia subcuticular, amphigenous, gregarious in small compact groups, 0.3–0.8 mm. across, conspicuous, applanate, 38–64 by 88–115  $\mu$ .

II. Primary uredinia amphigenous, more commonly hypophylloous, in more or less circular groups, 0.5–1.5 mm., surrounding the pycnia, when infection involves a vein more elongate, to 5 mm. or more, cinnamon brown, early naked, pulverulent, ruptured epidermis noticeable; urediniospores obovate, broadly ellipsoid or occasionally pyriform, 15–18 by 25–31  $\mu$ ; wall colorless or slightly tinted, 1.5–2.5  $\mu$  thick, apex thickened, 3–5.5  $\mu$ , sparsely and rather strongly echinulate, pores 3, slightly super-equatorial.

II. Secondary uredinia few, scattered, small, round, 0.2–0.5 mm. across, chiefly epiphyllous, otherwise like the primary uredinia.

*Croton* sp. Therezopolis, Rio de Janeiro, Brazil, Oct. 15, 1921, 1221.

This primary *Uredo* suggests relationship with *Bubakia*. It appears amply distinct from all the other Holway collections

and does not answer to the description of *Uredo Crotonis* P. Henn. It is possible that it may be the primary stage of *Bubakia mexicana* Arth., but that species has not been recognized in South America. It would appear that there are more species of rusts on *Croton* than has been supposed. Their interrelationship cannot be settled till more material is available, especially of collections with teliospores.

179. **Uromyces Actinostemonis** Jackson & Holway, sp. nov.

II. Uredinia amphigenous, chiefly hypophyllous, gregarious in groups 0.5-1.5 mm. across on discolored spots, often confluent, occasionally locally systemic in actively growing tissues and then occurring evenly distributed on all parts, golden brown, small, irregularly circular, 0.2-0.3 mm. across, tardily naked, pulverulent, ruptured epidermis noticeable; urediniospores ellipsoid or obovoid, small, 12-14 by 15-19  $\mu$ , wall colorless, 1.5-2  $\mu$  thick, finely and closely echinulate, slightly more prominently so toward upper half of spore; pores obscure.

III. Teliospores in the uredinia, obovoid or oblong, 12-20 by 30-44  $\mu$ , rounded above, rounded or somewhat narrowed below; wall uniformly thin, 1  $\mu$  or less, colorless, smooth, germinating at once with no evidence of germ pore; pedicel colorless, short.

*Actinostemon concolor* Muell. Gavea, Rio de Janeiro, Brazil, Sept. 7, 1921, 1093; Bom Successo, Rio de Janeiro, Sept. 13, 1921, 1107; Copacabana, Rio de Janeiro, Brazil, Sept. 21, 1921, 1140.

180. **UROMYCES ANDINUS** P. Magn. Ber. Deutsch. Bot. Ges. 11: 48. 1893.

*Euphorbia portulacoides* L. Termas de Chillan, Chile, Dec. 27, 1919, 250.

This appears to be a short cycled form. The *Aecidium*, *A. hypsophilum* Speg. (see No. 168) often found associated with it is presumably the aecial stage of a heteroecious species with the diplont perhaps on Fabaceae. It is possible, however, that it may prove to be an *Endophyllum*. *U. hypsophilus* Speg. is probably a synonym.

181. **UROMYCES CISNEROANUS** Speg. Anal. Soc. Ci. Argent. 10: 134. 1880.

*Uredo Cisneroana* Speg. Anal. Soc. Ci. Argent. 17: 119. 1884.

*Sapium* sp. Therezopolis, Rio de Janeiro, Brazil, Oct. 15, 1921, III, 1219, II, 1223; Campos do Jordão, São Paulo, Brazil, Apr. 26, 1922, III, 1772; Reserva Florestal, Itatiaya, Brazil, May 14, 1922, III, 1854.

This characteristic species has previously been reported only from Argentina and Paraguay.

182. *UROMYCES PROËMINENS* (DC.) Pass. Rab. Fungi Eur. 1795. 1873.

*Uredo proëminens* DC. Fl. Fr. 2: 235. 1805.

*Trichobasis euphorbiaecola* Berk. & Curt. Jour. Linn. Soc. 10: 357. 1869.

*Uromyces Euphorbiae* Cooke & Peck; Peck, Ann. Rept. N. Y. State Mus. 25: 90. 1873.

*Uromyces euphorbiicola* Tranz. Ann. Myc. 8: 8. 1910.

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*Euphorbia heterophylla* L. Santa Clara above Lima, Peru, July 23, 1920, II, III, 789.

*Euphorbia hirta* L. Lapa, São Paulo, Brazil, March 3, 1922, I, 1608.

*Euphorbia hypericifolia* L. Riobamba, Ecuador, Aug. 11, 1920, I, 871.

*Euphorbia lasiocarpa* Klotsch. Santa Clara above Lima, Peru, July 23, 1920, II & III, 787; Cochabamba, Bolivia, Feb. 27, 1920, II, III, 340.

*Euphorbia thymifolia* L. Sorata, Bolivia, Apr. 11, 1920, II & III, 501; La Paz, Bolivia, Apr. 3, 1920, II, III, 494.

*Euphorbia* sp. Huigra, Chimborazo, Ecuador, Aug. 6, 1920, I, 854; Cochabamba, Bolivia, March 13, 1920, II, III, 405.

183. *Uromyces tolerandus* Jackson & Holway, sp. nov.

III. Telia hypophylloous, chestnut brown, scattered or gregarious in groups 3 mm. across, round, 0.5–1 mm., tardily naked, pulverulent, ruptured epidermis conspicuous; teliospores ellipsoid, 18–22 by 27–38  $\mu$ , rounded below, acute at apex; wall chestnut brown, 2–3  $\mu$  thick, acute apex thickened 5–8  $\mu$ , finely, evenly, and inconspicuously verrucose, pedicel colorless, equalling the spore or shorter.

*Manihot* sp. Reserva Florestal, São Paulo, Brazil, May 9, 1922, 1827.

No uredinia or urediniospores were found in this collection. The aspect, however, is not that of a micro-form. The species appears to differ sufficiently from any of the numerous species recorded on this and related hosts.

#### SPECIES ON ANACARDIACEAE

184. *UREDO RHOMBICA* Speg. Anal. Soc. Ci. Argent. 17: 124. 1884.

*Astronium* sp. Rio de Janeiro, Brazil, Sept. 14, 1921, 1111; Jacarepagua, Rio de Janeiro, Brazil, Nov. 16, 1921, 1309.

A characteristic species easily identified by the rhomboid urediniospores. It appears to have been previously reported only from Paraguay.

#### SPECIES ON HIPPOCRATACEAE

185. *Aecidium Pereskiae* Jackson & Holway, sp. nov.

0. Pycnia epiphyllous, gregarious in a small group surrounded by aecia, prominent, deep seated, irregularly globoid or pyriform, 135–165  $\mu$  in diameter, ostiolar filaments present, not prominent.

I. Aecia epiphyllous, densely gregarious on somewhat hypertrophied discolored spots, surrounding the pycnia in a group 3–5 mm. in diameter, deep seated, bullate, small, 275  $\mu$  in diameter; peridium cupulate with margin erose or occasionally cylindrical, firm, white; peridial cells rhomboidal, 6–10 by 24–38  $\mu$ , outer wall 2.5–3  $\mu$  thick, smooth, inner wall 1.5–2.5  $\mu$ , prominently verrucose-tuberculate; aeciospores irregularly globoid or broadly ellipsoid, 25–38 by 25–40  $\mu$ ; wall thin, 1–1.5  $\mu$ , colorless, closely and finely verrucose.

*Pereskia grandifolia* Haw. Nictheroy, Rio de Janeiro, Brazil, Nov. 15, 1921, 1308 (type).

*Pereskia* sp. Friburgo, Rio de Janeiro, Brazil, Jan. 3, 1922, 1452.

Sections of this distinct species show a lining layer of mycelium to the aecidial cavity which persists after the aecia open and which accounts for the bullate appearance.

186. *Uromyces Pereskiae* Jackson & Holway, sp. nov.

II. Uredinia epiphyllous, gregarious on discolored spots 1.5-2.5 mm. across which appear greenish in dried specimens, round, 0.2-0.3 mm. in diameter, bullate, deep seated, cinnamon brown, tardily naked, becoming pulverulent, long covered by the firm overarched epidermis; urediniospores somewhat irregularly ellipsoid or obovate, 22-26 by 34-41  $\mu$ ; wall golden brown, 1.5-2.5  $\mu$  thick, sparsely and finely echinulate; pores 3 or 4 in a broad equatorial band.

III. Telia like the uredinia, blackish brown; teliospores somewhat irregularly broadly ellipsoid, 22-26 by 30-38  $\mu$ , rounded or truncate below, obtuse above; wall chestnut brown, 1.5-2  $\mu$  thick, appearing smooth but with irregularly scattered hyaline tubercles, sometimes arranged in lines and often more prominent at apex; pore prominent at apex but wall not thickened above; pedicel colorless, short, usually deciduous.

*Pereskia grandifolia* Haw. Fonseca, Nictheroy, Rio de Janeiro, Brazil, Sept. 18, 1921, 1123.

It is quite possible that this *Uromyces* is connected with the *Aecidium* described above as *Aecidium Pereskiae*. There is no evidence of the connection except that they are both collected in the same region and on the same host. It seems best, until more positive evidence is available of their identity, to describe the two forms as independent species.

## SPECIES ON SAPINDACEAE

187. *PUCINIA ARECHAVELATAE* Speg. Anal. Soc. Ci. Argent. 12: 67. 1881.

*Uromyces pervius* Speg. Anal. Soc. Ci. Argent. 17: 94. 1884.

*Uromyces aeruginosus* Speg. Revista Argent. Hist. Nat. 1: 20. 1891.

*Micropuccinia Arechavelatae* Arthur & Jackson, N. Am. Fl. 8: 541. 1922.

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*Cardiospermum Halicacabum* L. Huigra, Prov. Chimborazo, Ecuador, Aug. 3, 1920, 821; Pinheiros, São Paulo, Brazil, March 9, 1922, 1621.

*Serjania cuspidata* Camb. Bom. Successo, Rio de Janeiro, Brazil, Sept. 13, 1921, 1106; Gavea, Rio de Janeiro,

Brazil, Sept. 8, 1921, 1097; Fonseca, Nictheroy, Rio de Janeiro, Brazil, Sept. 18, 1921, 1121; Jacarépaguá, Rio de Janeiro, Brazil, Nov. 16, 1921, 1310.

*Serjania* sp. Santo Amaro, São Paulo, Brazil, Feb. 16, 1922, 1565; São Paulo, Brazil, Jan. 22, 1922, 1488; Juiz de Fora, Minas Geraes, Brazil, Dec. 17, 1921, 1408.

*Sapindaceae* (unidentified). Rio de Janeiro, Aug. 9, 1921, 1005; Aug. 10, 1921, 1010, Nov. 14, 1921, 1304; Nictheroy, Rio de Janeiro, Brazil, Aug. 18, 1921, 1052; Copacabana, Rio de Janeiro, Brazil, Sept. 21, 1921, 1141; Bello Horizonte, Minas Geraes, Brazil, Nov. 27, 1921, 1345, Dec. 1, 1921, 1352; Juiz de Fora, Minas Geraes, Brazil, Dec. 17, 1921, 1400, 1406; Campinas, São Paulo, Brazil, Apr. 3, 1922, 1695.

This characteristic microform has a wide distribution in South and Central America, as well as in the West Indies.

#### SPECIES ON RHAMNACEAE

188. *PUCCINIA GOUANIAE* Holway, Ann. Myc. 3: 21. 1905.

*Uredo Gouaniae* Lagerh. Cf. Sydow, Monog. Ured. 4: 574. 1924.

*Bullaria Gouaniae* Arthur & Mains, N. Am. Fl. 7: 487. 1922.

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*Gouania polygama* (Jacq.) Urb. Therezopolis, Rio de Janeiro, Brazil, Oct. 1, 1921, 1179.

*Gouania corylifolia* Raddi. Campinas, São Paulo, Brazil, Apr. 4, 1922, 1698.

This and the following species have apparently not been previously recognized in South America except for a single collection from Colombia (Toro 293). The collections involved have been compared with authentic material and we have no hesitancy in assigning them to the North American species.

189. *PUCCINIA INVAGINATA* Arth. & Johnston, Mem. Torrey Club 17: 146. 1918.

*Uredo Gouaniae* Ellis & Kelsey, Bull. Torrey Club 24: 209, 1897 (not *P. Gouaniae* Holway. 1905).

*Bullaria invaginata* Arth. & Mains, N. Am. Fl. 7: 488. 1922.

*Gouania* sp. Juquery, São Paulo, Brazil, June 12, 1922,  
1959.

190. PUCCINIA PARAENSIS Diet. Ann. Myc. 6: 96. 1908.

*Gouania Blanchetiana* Mig. Taquara, Rio de Janeiro, Bra-  
zil, Aug. 30, 1921, 1084.

A very characteristic brachy-form originally described on *Gouania pyrifolia* (?) from Marco, Para, Brazil. The primary uredinia occur on slightly hypertrophied spots often extending along the veins of the leaf. They are closely grouped, often confluent and occur on both sides of the leaf. Pycnia seem not to have been described but occur abundantly among the primary uredinia. They are amphigenous, inconspicuous, deep seated, globoid or nearly so, 120–140 by 140–160  $\mu$ , ostiolar filaments barely protruding.

The secondary uredinia and telia occur scattered on the under side of the leaves. The teliospore wall is often quite colorless, and the teliospores germinate as soon as mature.

#### SPECIES ON VITACEAE

191. ENDOPHYLLUM GUTTATUM (Kunze) Sydow, Ann. Myc. 17:  
179. 1920.

*Aecidium guttatum* Kunze in Weigelt exsicc. sine No. 1827.

*Aecidium circumscripum* Schw.; Berk. & Curt. Jour. Phil.  
Acad. Sci. II. 2: 283. 1853.

*Aecidium Cissi* Wint. Hedwigia 23: 168. 1884.

*Endophyllum circumscripum* Whetzel & Olive, Ann. Jour. Bot.  
4: 49. 1917.

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*Cissus sicyoides* L. Guayaquil, Ecuador, July 30, 1920, 795.

In assigning these collections to the *Endophyllum* the usual practice has been followed. In view of the probable origin of species of *Endophyllum* (see Jackson, H. S., Mem. Torrey Club 18: 1–108. 1931) it seems reasonable to expect that an unconnected *Aecidium* of a heteroecious rust, as will the *Endophyllum* derived from it, may both occur on this host.

192. PHAKOPSORA VITIS (Thüm.) Sydow, Hedwigia **38**: 141.  
1899.

*Uredo Vitis* Thüm. Pilze Weinst. 182. 1878.

*Physopella Vitis* Arth. Résult Sci. Cong. Bot. Vienne 338.  
1906.

*Vitis* sp. cult. Cuenca, Ecuador, Sept. 10, 1920, 975.

SPECIES ON TILIACEAE

193. **Didymopsora Triumfettae** Jackson & Holway, sp. nov.

0. Pycnia not seen, probably not formed.

III. Telia hypophyllous, occurring singly or in closely aggregated groups of 3–10 sori on slightly hypertrophied areas, groups usually more or less circular in outline, when associated with leaf veins more elongate; individual telia deep seated, waxy, forming cylindrical or terete columns to 1 mm. in height, 200–275  $\mu$  in diameter at base; peridium absent; teliospores catenate, two celled, without intercalary cells, 8–12 by 27–38  $\mu$ , slightly or not constricted at septum, two celled character not always evident; wall thin, colorless, apparently swelling considerably, germinating at once from apex to base of column.

*Triumfetta longicornis* St. Hil.? Juiz de Fora, Minas Geraes, Brazil, Dec. 17, 1921, 1405.

This very distinct species might easily be confused in the field with *Pucciniosira pallidula* (Speg.) Lag. The telia are more waxy in consistency and develop considerably longer than in that species, and are of considerably greater diameter at the base. Microscopically the two species are quite different. In this species there is no evidence of a peridium and a most careful search has failed to reveal the presence of intercalary cells, which are consistently present and quite easily demonstrated in the *Pucciniosira*.

I have assigned the species to *Didymopsora* as it seems to fit the characters of that genus better than any other. The two celled character of the spore is in some mounts very evident, in others one obtains the impression of chains of one celled spores suggesting *Endophylloides* or *Chionothrix*.

Elsewhere (Mem. Torrey Club **18**: 78–80. 1931) I have dis-

cussed the possible origin of *Pucciniosira* and similar genera and pointed out their resemblance to *Endophyllum*. In the species under discussion it seems possible to account for its origin from an *Endophyllum*-like species in which the spores have become vertically and laterally adherent due to the gelatinization of the cell wall, the peridium has been lost or has reverted to the ancestral condition and retained the spore function, and in which the intercalary cell cut off from the spore initial also becomes functional as a spore cell. It is noticeable that this species and the next as well as many other species in these and related genera have an *Aecidium*-like habit as shown by the deep seated character of the sorus initial and the tendency to be aggregated in close groups often on slightly hypertrophied areas.

194. PUCCINIOSIRA PALLIDULA (Speg.) Lagerh. Tröms. Mus. Aarsh. **16**: 122. 1894.

*Coleosporium (?) pallidulum* Speg. Anal. Soc. Ci. Argent. **17**: 95. 1884.

*Pucciniosira Triumfettae* Lagerh. Ber. Deuts. Bot. Ges. **9**: 344. 1891.

*Aecidium Triumfettae* P. Henn. Hedwigia **35**: 259. 1896.

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*Triumfetta semitriloba* L. Villa Aspiazú, Prov. Sur Yungas, Bolivia, May 31, 1920, 688; Friburgo, Brazil, Jan. 5, 1922, 1459.

*Triumfetta* sp. Guayaquil, Ecuador, July 31, 1920, 798; Jardim Bot., Rio de Janeiro, Brazil, Aug. 11, 1921, 1017.

A widely distributed species in South and Central America and the West Indies.

195. UREDO LUEHEAE Speg. Anal. Mus. Nac. Hist. Buenos Aires **23**: 31. 1912.

*Luehea* sp. Cantareira, São Paulo, Brazil, May 30, 1922, 1919.

This species seems to have been reported previously only from the type locality near Yuto, Juquy, Argentina.

## SPECIES ON MALVACEAE

196. CEROTELIUM DESMIUM (Berk. & Br.) Arth. N. Am. Fl. 7: 698. 1925.

*Aecidium desmum* Berk. & Br. Jour. Linn. Soc. 14: 95. 1875.

*Uredo Gossypii* Lag. Jour. Myc. 7: 48. 1891.

*Kuehneola Gossypii* Arth. N. Am. Fl. 7: 187. 1912.

*Kuehneola Gossypii* Butler, Fung. Dis. Pl. 363. 1918.

*Gossypium* sp. Nictheroy, Rio de Janeiro, Brazil, Nov. 15, 1921, 1307.

A well known species occurring throughout the world where cotton is grown.

197. CEROTELIUM MALVICOLUM (Speg.) Dietel in Engler, Nat. Pfl. II. 6: 57. 1928.

*Uredo malvicolus* Speg. Anal. Soc. Ci. Argent. 17: 124. 1884.

*Rostrupia praelonga* Speg. Contr. Fl. Ventana 83. 1896.

*Kuehneola malvicolus* Arth. N. Am. Fl. 7: 187. 1912.

*Pavonia sepium* St. Hill. Copacabana, Rio de Janeiro, Brazil, Sept. 21, 1921, 1139.

*Pavonia speciosa* H.B.K. Villa Augusta, São Paulo, Brazil, Feb. 25, 1922, 1598.

*Pavonia spinifex* Cav. São Paulo, Brazil, Jan. 19, 1922, 1480.

*Malvaviscus* sp. (cult.). Rio de Janeiro, Brazil, Nov. 12, 1921, 1293, Dec. 20, 1921, 1410.

198. PUCCINIA INTERVENIENS (Peck) Bethel; Blasdale, Univ. Calif. Pub. Bot. 7: 119. 1919.

*Roestelia interveniens* Peck, Bull. Torrey Club 10: 74. 1883.

*Aecidium Malvastri* P. Henn. Hedwigia 36: 216. 1897.

*Aecidium Sphaeralceae* Speg. Anal. Mus. Nac. Buenos Aires 19: 322. 1909.

*Allodus interveniens* Arthur & Orton, N. Am. Fl. 7: 797. 1927.

*Malvastrum capitatum* (Cav.) Griseb. Cochabamba, Bolivia, March 11, 1920, 397.

*Malvastrum* sp. La Falda, Cordoba, Argentina, Aug. 21, 1922, 2037.

*Sphaeralcea obtusifolia* Don. Zapallar, Chile, Sept. 22, 1919, 61.

*Sphaeralcea* sp. Viña del Mar, Chile, Sept. 10, 1919, 17.

These collections of aecidia were reported by Arthur (Proc. Am. Phil. Soc. **64**: 203. 1925) as the aecial stage of the heteropspis *Puccinia interveniens* which has telia on the grass genera *Nasella* and *Stipa*. The collections are reported here to make the record of malvaceous rusts in the Holway collections complete.

199. *PUCCINIA EXILIS* Sydow, Monog. Ured. **1**: 481. 1903.

*Pavonia rosea* Schl. Lapa, São Paulo, Brazil, June 4, 1922, 1940.

This species seems to have been reported previously from South America only in connection with the original description. The type collection is from Brazil but no locality is given. The species is also known from Guatemala in Central America.

200. *PUCCINIA HETEROGENA* Lagerh. Jour. Myc. **7**: 47. 1891.

*Althaea* sp. (cult.). Cuzco, Peru, June 29, 1920, 739.

*Malvaceae* (cult.). Quito, Ecuador, Aug. 26, 1920, 946; Biblian, Prov. de Cañar, Ecuador, Sept. 19, 1920, 965.

One of the above listed collections (946) is from the type locality for this distinct species which seems not to have been previously reported except from Ecuador.

201. *PUCCINIA HETEROSPORA* Berk. & Curt.; Berk. Jour. Linn. Soc. **10**: 356. 1868.

*Uromyces malvacearum* Speg. Anal. Soc. Ci. Argent. **12**: 72. 1881.

*Uromyces malvicola* Speg. Anal. Soc. Ci. Argent. **17**: 94. 1884.

*Micropuccinia heterospora* Arth. & Jackson, Arth. Bull. Torrey Club **48**: 41. 1921.

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*Sida cordifolia* L. Campinas, São Paulo, Brazil, Apr. 2, 1922, 1687; Santa Anna, São Paulo, Brazil, Feb. 22, 1922, 1589.

*Sida paniculata* L. Copacabana, Rio de Janeiro, Brazil,  
Sept. 21, 1921, 1132.

*Sida spinosa* L. Hacienda Anacuri, Prov. Nor Yungas,  
Bolivia, June 5, 1920, 725.

*Sida tomentosa* Mig. Friburgo, Rio de Janeiro, Jan. 6, 1922,  
1462.

*Sida urens* L. Hacienda La Florida, Prov. Sur Yungas,  
Bolivia, May 28, 1920, 674; São Caetano, São Paulo, Bra-  
zil, March 8, 1922, 1618; Prata, São Paulo, Brazil, Apr.  
7, 1922, 1705.

*Wissadula hernandoioides* (L'Hér.) Garche. Bello Horizonte,  
Minas Geraes, Brazil, Nov. 22, 1921, 1326.

202. **PUCCINIA MALVACEARUM** Bert. Mont. in Gay Fl. Chil. 8:  
43. 1852.

*Althaea* (cult.). Olmue, Chile, Sept. 11, 1919, 21.

*Malva* sp. Viña del Mar, Chile, Sept. 5, 1919, 5; San Felipe,  
Chile, Sept. 25, 1919, 66.

203. **Puccinia platyspora** (Speg.) Jackson & Holway, comb. nov.

*Uromyces platysporus* Speg. Anal. Mus. Nac. Buenos Aires  
6: 218. 1899.

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*Sphaeralcea* sp. La Falda, Argentina, Aug. 21, 1922, 2036.

The above specimen is from the region where this species has  
been reported. It seems to be distinct. A few two celled telio-  
spores are present resembling somewhat the teliospores of *P.  
Sherardiana*. The great majority of the spores are one celled,  
however.

204. **PUCCINIA SHERARDIANA** Koern. Hedwigia 16: 19. 1877.

*Abutilon sylvaticum* (Cav.) Schum. Sorata, Bolivia, Apr. 19,  
1920, 555.

*Malva parviflora* L. Zapallar, Chile, Jan. 31, 1920, 305.

*Malvastrum coromandelianum* (L.) Garche. Rio de Janeiro,  
Brazil, Aug. 12, 1921, 1022; Juiz de Fora, Minas Geraes,  
Brazil, Dec. 17, 1921, 1409; Campinas, São Paulo, Brazil,  
Apr. 4, 1922, 1700.

*Malvastrum* sp. Sorata, Bolivia, Apr. 14, 1920, 518.

*Sida rhombifolia* L. Cochabamba, Bolivia, Feb. 26, 1920,  
335.

SPECIES ON HYPERICACEAE

205. **UROMYCES HYPERICI-FRONDOSI** (Schw.) Arth. Bull. Minn. Acad. Nat. Sci. 2: 15. 1883.

*Aecidium Hyperici-frondosi* Schw. Schr. Nat. Ges. Leipzig 1: 68. 1822.

*Uromyces pachycephalus* Neger, Anal. Univ. Chile 93: 785. 1896.

*Hypericum brasiliense* Choisy. Therezopolis, Rio de Janeiro, Brazil, Oct. 12, 1921, 1215; Petropolis, Rio de Janeiro, Brazil, Nov. 3, 1921, 1274; Alto da Serra, São Paulo, Brazil, Jan. 28, 1922, 1502.

*Hypericum chilense* Gay. Panimavida, Chile, Dec. 15, 1919, 235; Recinto, Chile, Jan. 9, 1920, 280.

*Hypericum* sp. Sorata, Bolivia, Apr. 19, 1920, 545; Ouro Preto, Minas Geraes, Brazil, Dec. 9, 1921, 1379; Friburgo, Rio de Janeiro, Jan. 5, 1922, 1460; Campos do Jordão, São Paulo, Brazil, Apr. 20, 1922, 1738.

SPECIES ON CLUSEACEAE

206. **Uredo Zarumae** Jackson & Holway, sp. nov.

II. Uredinia hypophyllous, closely gregarious in large areas 2–5 cm. across, evidently locally systemic, small, irregular, 0.2–0.4 mm. across, yellowish, early naked, pulverulent, ruptured epidermis conspicuous; urediniospores short stipitate, irregularly ellipsoid or oblong, 16–25 by 30–40  $\mu$ ; wall colorless, thin, 1–1.5  $\mu$ , closely, evenly and conspicuously verrucose.

*Clusia multiflora* H.B.K.? N. of Zaruma, Ecuador, Sept. 20, 1920, 996.

A very distinct species the sori of which occur closely gregarious in large irregular patches on the underside of the leaves evidently from an infection which becomes locally systemic. Sections indicate that the sori are intraepidermal and covered by the outer wall of the epidermal cells and the cuticle.

## SPECIES ON VIOLACEAE

207. PUCCINIA VIOLAE (Schum.) DC. Fl. Fr. 6: 62. 1815.

*Aecidium Violae* Schum. Enum. Pl. Saell 2: 224. 1803.

*Viola maculata pubescens* Reiche. Temuco, Chile, Nov. 1, 1919, 152, Dec. 5, 1919, 197; Termas de Chillan, Chile, Dec. 31, 1919, 259.

*Viola* sp. Recinto, Chile, Jan. 10, 1920, 285.

## SPECIES ON LOASACEAE

208. UREDO FLORIDANA Sydow, Hedwigia 40: 129. 1901.

*Blumenbachia lateritia* Hook f. Sorata, Bolivia, Apr. 17, 1920, 540.

*Blumenbachia* sp. Huigra, Chimborazo, Ecuador, Aug. 3, 1920, 819.

This species has previously been reported only on the genus *Mentzelia* from Florida and Lower California in North America. The hosts are closely related and it seems best to record it as above as we can detect no essential difference between our collections and the North American material.

## SPECIES ON CACTACEAE

209. AECIDIUM OPUNTIAE P. Magn. Ber. Deut. Bot. Ges. 16: 151. 1898.

*Opuntia sulphurea* Don. Cochabamba, Bolivia, March 1, 1920, 357.

Arthur, in his account of the South American grass rusts (Proc. Am. Phil. Soc. 64: 189. 1925), lists this aecidium as the aecial stage of *Puccinia Opuntiae* (Magn.) Arth. & Holway. The suggested connection of this aecidium with uredinia and telia on *Bouteloua simplex* Lag. is based on field observations only. While this surmise is doubtless correct, it seems best for the purposes of this account to list the collection as above.

## SPECIES ON LYTHRACEAE

210. Uredo cupheicola Jackson & Holway, sp. nov.

II. Uredinia hypophylloous, scattered or occasionally gregarious, round, 0.2-0.5 mm. across, cinnamon brown, tardily naked,

somewhat bullate, pulverulent, ruptured epidermis conspicuous; urediniospores irregularly ellipsoid or obovoid, 16–22 by 28–36  $\mu$ ; wall thin, 1–1½  $\mu$ , cinnamon brown, often lighter in color in lower half of spore, closely and finely verrucose; pores three approximately equatorial.

*Cuphea dipetala* (L. f.) Koehne. Sorata, Bolivia, Apr. 16, 1920, 531.

The sori of this clearly distinct species appear to have a somewhat indefinite pseudoperidium. The spore characters serve to separate it definitely from *Uredo Cupheae* P. Henn.

### 211. *Uredo Lafoenseae* Jackson & Holway, sp. nov.

II. Uredinia subepidermal, hypophylloous, scattered or gregarious, cinnamon brown, round, 0.2–0.4 mm., tardily naked, somewhat bullate, becoming pulverulent, ruptured epidermis conspicuous; urediniospores somewhat irregularly ellipsoid or obovoid, 16–19 by 22–31  $\mu$ , wall cinnamon brown, thin, 1  $\mu$  or less, moderately and finely echinulate, pores three, approximately equatorial.

*Lafoensis Pacari* St. Hil. Campos do Jordão, São Paulo, Brazil, Apr. 26, 1922, 1774.

This species differs from the preceding primarily in spore size, and from *Uredo Cupheae* P. Henn. in the somewhat larger spores and in the character of the wall markings. In *Uredo Cupheae* P. Henn. the markings are much more closely placed.

## SPECIES ON MYRTACEAE

### 212. *Puccinia Psidii* Winter, Hedwigia 23: 171. 1884.

*Caeoma Eugeniarum* Link, Sp. Plant 2: 29. 1825.

*Uredo neurophila* Speg. Anal. Soc. Ci. Argent. 17: 122. 1884.

*Uredo subneurophila* Speg. Anal. Soc. Ci. Argent. 17: 123. 1884.

*Uredo flavidula* Wint. Hedwigia 24: 260. 1885.

*Uredo Myrtacearum* Paz. Hedwigia 29: 159. 1890.

*Uredo Eugeniarum* P. Henn. Hedwigia 34: 337. 1895.

*Aecidium Glaziovii* P. Henn. Hedwigia 36: 216. 1897.

*Puccinia Jambosae* P. Henn. Hedwigia 41: 105. 1902.

*Uredo Goeldiana* P. Henn. Hedwigia Beibl. 42: 188. 1903.

*Uredo Myrciae* Mayor, Mem. Soc. Neuch. Sci. Nat. 5: 590. 1913.

*Puccinia Jambulana* Rangel, Bol. Agr. São Paulo **21**: 37.  
1920.

*Puccinia subneurophila* Speg. Anal. Mus. Nac. Hist. Nat.  
Buenos Aires **31**: 32. 1922.

*Puccinia neurophila* Speg. Rev. Argent. Bot. **1**: 120. 1925.

*Eugenia* sp. Nictheroy, Rio de Janeiro, Brazil, Nov. 15,  
1921, 1306.

*Myrcia* sp. Campos do Jordão, São Paulo, Brazil, Apr. 26,  
1922, 1775; Juquery, São Paulo, Brazil, Feb. 2, 1922,  
1526.

*Psidium Guajava* L. Rio de Janeiro, Brazil, Nov. 14, 1921,  
1302.

*Psidium* sp. Barbacena, Minas Geraes, Brazil, Dec. 12,  
1921, 1383.

*Myrtaceae*, genus & sp. unknown. Bello Horizonte, Minas  
Geraes, Brazil, Nov. 26, 1921, 1342.

I have followed the combined treatment of Arthur (N. Am. Fl. **7**: 488. 1922), Sydow (Monog. Ured. **4**: 571. 1924), and Spiegazinii (Rev. Argent. Bot. **1**: 120, 127. 1925) in listing the synonyms of this much named species. Specimen No. 1775 on *Myrcia* bears teliospores; all the other collections are of uredinia; the teliospores on our specimen differ somewhat from the usual description, but we hesitate to erect a new name. They are irregularly ellipsoid or obovate, 18–20 by 32–48  $\mu$ , occasionally three celled and often with septa oblique, usually slightly constricted at septum and germinating at once; wall colorless, 1–1.5  $\mu$  thick, usually not thickened above but in occasional spores to 9  $\mu$ , smooth; pedicel colorless, equalling the spore, or more commonly shorter, often obliquely inserted.

### 213. *Uredo seclusa* Jackson & Holway, sp. nov.

II. Uredinia hypophyllous, scattered, or more commonly gregarious on small purplish spots, small, irregularly circular in outline, cinnamon brown, tardily naked, pulverulent, ruptured epidermis conspicuous; urediniospores somewhat irregularly ellipsoid or obovoid, 15–20 by 24–32  $\mu$ ; wall thin, 1  $\mu$  or less, cinnamon brown, moderately and finely echinulate, the pores two or three, super-equatorial.

*Myrtaceae* sp. Villa Prudente, São Paulo, Brazil, May 31, 1922, 1925.

This *Uredo* is very distinct from the uredinia stage of *Puccinia Psidii* Wint. and appears to differ from any previously described.

#### SPECIES ON ONAGRACEAE

214. PUCCINIA EPILOBII-TETRAGONI (DC.) Wint. in Rab. Krypt. Fl. 1: 214. 1881.

*Uredo vagans Epilobii-tetragonii* DC. Fl. Fr. 2: 228. 1805.

?*Aecidium Oenotherae* Mont. in Gay, Hist. Chile 8: 37. 1852.

*Aecidium Gayophyti* Vize, Grevillea 7: 12. 1878.

*Puccinia Boisduvaliae* Peck, Bot. Gaz. 7: 45. 1882.

*Puccinia Gayophyti* Peck, Bot. Gaz. 7: 56. 1882.

*Puccinia Sphaerostigmatis* Dietel & Neger in Engl. Bot. Jahrb. 22: 353. 1896.

*Puccinia luxurians* Dietel & Neger in Engl. Bot. Jahrb. 24: 158. 1817.

*Puccinia Gayophyti* Speg. Anal. Mus. Nac. Buenos Aires III, 1: 63. 1902.

*Puccinia humilis* Speg. Rev. Arg. Bot. 1: 116-117. 1925.

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*Boisduvalia concinna* Spach. Panimávida, Chile, Dec. 15, 1919, 230; Baños de Canquenes, Rancagua, Chile, Jan. 13, 1920, 298.

*Epilobium andicolum* Haussk. La Paz, Bolivia, March 24, 1920, 453.

*Godetia Cavanillesii* Spach. Papudo, Chile, Sept. 19, 1919, 50.

*Godetia* sp. San Jose de Maipo, Chile, Oct. 6, 1919, 91.

*Lavauxia mutica* Spach. Papudo, Chile, Sept. 18, 1919, 43; Panamavida, Chile, Dec. 9, 1919, 205.

*Lavauxia* sp. Viña del Mar, Chile, Sept. 7, 1919, 14.

*Oenothera mollissima* L. Panimávida, Chile, Dec. 13, 1919, 224.

*Oenothera* sp. Constitucion, Chile, Oct. 17, 1919, 121; Quito, Ecuador, Aug. 23, 1920, 939.

*Sphaerostigma tenuifolium* Spach. Papudo, Chile, Sept. 23, 1919, 65.

*Sphaerostigma* sp. Pichilemu, Chile, Oct. 12, 1919, 107.

I have followed the treatment of Bisby (Am. Jour. Bot. 3: 527-561. 1916) in assigning all these collections to the above species. As here considered, this species is apparently abundant in both North and South America.

#### SPECIES ON UMBELLIFERAE

215. AECIDIUM HYDROCOTYLINUM Speg. Anal. Mus. Nac. Buenos Aires 19: 321. 1909.

*Hydrocotyle Poepigii* DC. Temuco, Chile, Nov. 1, 1919, 154, Dec. 7, 1919, 203.

*Hydrocotyle* sp. Valdivia, Chile, Nov. 13, 1919, 175.

A comparison of these collections with North American material assigned to *Uromyces Scirpi* shows that they are not the same. The type of *A. hydrocotylinum* Speg. has not been seen, but it seems best to record the above collections under that name. It is entirely possible that this is the *Aecidium* of *Puccinia Hydrocotyles*, but the life history of that species is unknown. The fact that *P. Hydrocotyles* has a wide distribution in both North and South America and has been frequently collected without its life history becoming certainly known would hardly support the view that an *Aecidium* is present in the life history.

216. PUCCINIA HYDROCOTYLES (Link) Cooke, Grevillea 9: 14. 1880.

*Caeoma Hydrocotyles* Link in Willd. Sp. Pl. 6: 22. 1825.

*Trichobasis Hydrocotyles* Cooke, Jour. Bot. 2: 343. 1864.

*Uredo Hydrocotyles* Bertero, Mont. Ann. Sci. Nat. II, 3: 356. 1835.

*Uredo bonariensis* Speg. Anal. Soc. Ci. Argent. 9: 171. 1880.

*Aecidiolum Hydrocotyles* Speg. Anal. Soc. Ci. Argent. 12: 80. 1881.

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*Hydrocotyle aconitifolia* Rich. San Felipe, Prov. Sur Yungas, Bolivia, May 19, 1920, 626.

*Hydrocotyle bonariensis* Lam. Arequipa, Peru, July 11, 1920, 772; Gavea, Rio de Janeiro, Brazil, Sept. 8, 1921, 1094.

*Hydrocotyle Bonplandii* Rich. Quito, Ecuador, Aug. 18, 1920, 899.

*Hydrocotyle umbellata* L. Huigra, Prov. Chimborazo, Ecuador, Aug. 6, 1920, 850.

*Hydrocotyle Volkmanni* Phil. Panamavida, Chile, Dec. 11, 1919, 219.

*Hydrocotyle* sp. Quito, Ecuador, Aug. 15, 1920, 897; Therzopolis, Rio de Janeiro, Brazil, Sept. 28, 1921, 1158.

217. *Puccinia obscurata* Arth. & Holway; Arth. Am. Jour. Bot. 5: 477. 1918.

*Neonelsonia acuminata* (Benth.) C. & R. Quito, Ecuador, Aug. 18, 1920, 924.

This species is otherwise known only from the type locality in Guatemala.

218. *Uromyces mulini* Schroet. Hedwigia 35: 224. 1896.

*Uromyces mulini* Speg. Anal. Mus. Nac. Buenos Aires 6: 218. 1899.

*Uredo mulinicola* Speg. Anal. Mus. Nac. Buenos Aires 6: 235. 1899.

*Uromyces mulini* Schroet. var. *magellanica* Neger, Ofvers. Kongl. Vet.-Akad. Foch. 56: 746. 1899.

*Aecidium azorellae* Speg. Anal. Mus. Nac. Buenos Aires 6: 230. 1899.

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*Mulinum spinosum* (Cav.) Pers. Termas de Chillan, Chile, Dec. 29, 1919, 255.

A characteristic species first reported from South America by Leveille in 1846 as *Uredo cynappii* DC. The above collection includes both aecia and telia. The species is evidently an -opsis form.

219. *Puccinia discors* Jackson & Holway, sp. nov.

I. Pycnia amphigenous, gregarious in small groups, punctiform, deep seated, globose or ellipsoid, 75-85 by 75-100  $\mu$ , ostiolar filaments not protruding.

II. Primary uredinia amphigenous, surrounding the pycnia, secondary uredinia amphigenous or petiolicolous, scattered or occasionally gregarious, round, often more elongate when on

veins or petioles, early naked, cinnamon brown, pulverulent, ruptured epidermis conspicuous; urediniospores obovate or ellipsoid, 25–28 by 32–38  $\mu$ ; wall cinnamon brown, 2.5–3  $\mu$ , considerably thickened, 5–7.5  $\mu$  at apex, moderately and finely verrucose echinulate; pores 3, approximately equatorial.

III. Telia like the uredinia, light chestnut brown, pulverulent; teliospores broadly ellipsoid or oblong, 23–28 by 35–44  $\mu$ , rounded above and below, scarcely constricted at septum; wall light chestnut brown, 2.5–3  $\mu$  thick, slightly thickened, 4–5  $\mu$ , over pore at apex of upper cell and over pore of lower cell, which is usually situated half way between septum and pedicel, evenly, closely and finely verrucose; pedicel colorless, short, deciduous.

*Conium maculatum* L. Papudo, Chile, Sept. 19, 1919, 51;  
Zapallar, Chile, Sept. 22, 1919, 62 (type), Jan. 31, 1920,  
303.

A distinct brachy-form. Sections show that teliospores may occur in primary uredinia.

## 220. *Puccinia mundula* Jackson & Holway, sp. nov.

0. Pycnia amphigenous, petiolicolous or caulicolous, honey yellow, punctiform, closely grouped among the aecia, deep seated.

I. Aecia amphigenous, petiolicolous or caulicolous, more commonly hypophyllous, in close groups on somewhat hypertrophied spots, groups elongate when involving veins petioles or stems, round, 0.4–0.8 mm. in diam., bullate, pulverulent; peridium present but soon breaking up into individual cells which occur scattered among the spores, peridial cells in face view 25–32  $\mu$ , wall prominently and closely verrucose; aeciospores somewhat irregularly globoid or ellipsoid, 15–20 by 20–30  $\mu$ ; wall colorless, thin, 1  $\mu$  or less, closely and finely verrucose.

II. Uredinia hypophyllous, scattered, round, 0.3–0.5 mm. across, early naked, golden brown, pulverulent, ruptured epidermis not noticeable; urediniospores ovoid or ellipsoid, 19–21 by 25–30  $\mu$ ; wall colorless or slightly tinted golden brown, 2.5  $\mu$  thick, finely and closely verrucose, pores three, approximately equatorial.

III. Telia like the uredinia, pulverulent, light chestnut brown; teliospores ellipsoid or oblong, 20–23 by 32–38  $\mu$ , rounded above, rounded or somewhat narrowed or truncate below, slightly or not at all constricted at the septum; wall light chestnut brown, 1.5–2  $\mu$  thick, slightly thickened, 3–4  $\mu$  at pores, with sparsely placed elongated thickenings often arranged in longitudinal lines; pedicel colorless, short, deciduous.

*Osmorrhiza* sp. Pongo, Prov. Sur Yungas, Bolivia, May 18, 1920, 610.

A very distinct species, quite unlike *P. Philippii* Diet. & Neger. The aecia are of the sort often referred to as caeomoid. A peridium is present, however, as shown by sections. The peridial cells soon break apart and become scattered among the spores from which they are easily distinguished by their somewhat larger size and coarser wall markings. The markings of the teliospores are peculiar and easily overlooked, the effect is to give the margin of the spore a somewhat wavy appearance. The true nature of the thickenings is best seen in lacto-phenol.

221. PUCCINIA PHILIPPII Dietel & Neger, Engl. Bot. Jahrb. 22: 352. 1896.

*Aecidium Philippii* Speg. Bol. Acad. Nac. Ci. Cordoba 27: 355. 1924.

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*Osmorrhiza Berteri* DC. Concepcion, Chile, Oct. 26, 1919, 139; Peulla, Lago Todos los Santos, Chile, Nov. 30, 1919, 194.

*Osmorrhiza* sp. Temuco, Chile, Nov. 1, 1919, 153; Pani-mávida, Chile, Dec. 15, 1919, 232.

The first two specimens listed are on the same host as the type collection and from the same region. The species has also been collected in Argentina and Patagonia.

222. **Puccinia repentina** Jackson & Holway, sp. nov.

II. Uredinia not seen; urediniospores in the telia obovate, 21–25 by 30–37  $\mu$ ; wall golden brown, 2–2.5  $\mu$  thick, thickened at apex, 7–10  $\mu$ , and frequently also at base, moderately and finely echinulate, pores somewhat obscure, apparently three, approximately equatorial.

III. Telia hypophyllous, round, 0.3–0.5 mm. across, blackish brown, early naked, pulverulent, ruptured epidermis not conspicuous; teliospores somewhat irregularly ellipsoid or oblong, 23–28 by 32–45  $\mu$ , rounded above and below, scarcely constricted; wall chestnut brown, 2.5–3.5  $\mu$  thick, thickened slightly over pores, 4–6  $\mu$ , very finely and closely verrucose; pedicel colorless, short, deciduous.

*Arracacia xanthorrhiza* Bauer. Sorata, Bolivia, Apr. 22, 1920.  
563.

This species is quite different from others previously described on this host genus and does not appear to be the same as any reported on closely related hosts. The pore in the lower cell of the teliospore is usually close to the septum, sometimes slightly depressed. The wall markings are so fine that the spores appear nearly smooth in water mounts.

#### SPECIES ON CORNACEAE

223. PUCCINIA GRISELINIAE Pazschke, Hedwigia **35**: 52. 1896.  
*Griselia ruscifolia* Taub. Serra Itatiaya, São Paulo, Brazil, May 17, 1922, 1855.

The collection of this interesting micro-form was apparently made near the type locality. It is otherwise known only from the original collection (Ule, 2101) and one other (Ule, 1642) made at Serra Geral, Brazil.

#### SPECIES ON ERICACEAE

224. UREDO ANDROMEDAE Cooke, DeToni, in Sacc. Syll. Fung. **7**: 853. 1888.  
*Pernettya Pentlandii* DC. Sorata, Bolivia, May 7, 1920, 594.

This form is not unlike several North American collections on *Pieris* and *Xolisma*, which were originally named *Uredo Andromedae* by Cooke and are now assigned by Arthur, in the North American Flora Supplement, to *Pucciniastrum Myrtilli* (Schum.) Arth. There seems to be some reasonable basis for doubt that they belong with the latter species. Our assignment of the collection listed above to *Uredo Andromedae* is merely tentative.

#### SPECIES ON MYRSINACEAE

225. UROMYCES MYRSINES Diet. Hedwigia **36**: 26. 1897.  
*Uromyces Rhapaneae* P. Henn. Hedwigia **48**: 1. 1908.  
*Uromyces Usterianus* Diet. Ann. Myc. **6**: 96. 1908.

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*Icacorea* sp.? Poços da Caldas, São Paulo, Brazil, Apr. 10, 1922, 1721.

- Rapanea pseudocrenata* Maz.? Hacienda La Florida, Prov. Sur Yungas, Bolivia, May 26, 1920, 662; Villa Aspiazu, Prov. Sur Yungas, Bolivia, June 1, 1920, 695; Coroico, Prov. Nor Yungas, Bolivia, June 11, 1920, 730.
- Rapanea umbellata* (Mart.) Mez. Therezopolis, Rio de Janeiro, Brazil, Oct. 26, 1921, 1248.
- Rapanea* sp. Campos do Jordão, São Paulo, Brazil, Apr. 28, 1922, 1782.

This characteristic short cycle species has previously been reported only from Brazil. According to Sydow *U. usherianus*, originally described as on a member of the Myrtaceae, is really on Myrsine.

#### SPECIES ON GENTIANACEAE

##### 226. *Puccinia Lisianthi* Jackson & Holway, sp. nov.

II. Uredinia hypophyllous and caulicolous, gregarious, large, 0.5–1 mm., round or oval in outline, cinnamon brown, deep seated, tardily naked, pulverulent, long covered by the over-arching epidermal and subepidermal tissues; urediniospores obovoid or ellipsoid, 18–21 by 25–34  $\mu$ ; wall colorless or slightly tinted golden brown, 1–2  $\mu$  thick, rather closely and finely echinulate with smooth areas surrounding the pores; pores two, equatorial or slightly superequatorial.

III. Telia like the uredinia, compact, cinnamon brown; teliospores cylindrical or elongate terete, 14–18 by 44–56  $\mu$ , obtuse above, narrowed and truncate or less commonly rounded below, constricted at septum; wall colorless or slightly tinted golden brown, 1.5  $\mu$  thick, apex thickened 3–4  $\mu$ , smooth; pedicel colorless, equaling the spore or longer, broad at point of attachment, 5–6.5  $\mu$ , soon collapsing.

*Lisanthus elegans pedunculatus* Cham. & Schl. Ouro Preto, Minas Geraes, Brazil, Dec. 8, 1921, 1372.

An apparently distinct form in which the uredinia appear to be locally systemic. The uredinia are very characteristic, originating quite deeply in the tissues and covered by the epidermis and three or four layers of the rather compact spongy parenchyma. The hymenium of the sorus is flat as in those forms in which the sorus originates just beneath the epidermis. Teliospores are not abundant in this material but occasionally occur in sori essentially like the uredinia and germinate at once.

## SPECIES ON APOCYNACEAE

227. AECIDIUM OCHRACEUM Speg. Rev. Argent. Hist. Nac. Buenos Aires 1: 401. 1891.

*Tabernaemontana amygdalifolia* Jacq. Friburgo, Rio de Janeiro, Brazil, Jan. 5, 1922, 1458.

It is probable that the record from Paraguay of *A. ceraceum* Berk. & Br., made by P. Hennings (*Hedwigia* 35: 257. 1896), is an error for the above species. *A. ceraceum* is, according to Sydow (*Monog. Ured.* 4: 320. 1923), the aecial stage of *Puccinia Tabernaemontanae* Berk. & Br., which is known only from Ceylon, Natal and Zululand. The aeciospores of *A. ochraceum* Speg. are quite different, and it is probable that it is heteroecious.

228. ***Puccinia Mandevillae* Jackson & Holway, sp. nov.**

0. Pycnia not seen, probably not formed.

III. Telia hypophyllous, gregarious in small groups 1-4 mm. across, irregularly rounded, commonly confluent, early naked, compact, becoming pulvinate and cinereous through germination, cinnamon brown, ruptured epidermis at first noticeable; teliospores ellipsoid, clavate or oblong, 14-18 by 29-38  $\mu$ , rounded above, rounded or narrowed to pedicel below, slightly or not constricted at septum, which is ordinarily transverse, occasionally oblique; wall colorless or slightly tinted golden brown, 1-1.5  $\mu$  thick, thickened to 3  $\mu$  at apex, smooth; pedicel colorless, once to twice the length of the spore, 6-7  $\mu$  broad at point of attachment, soon collapsing.

*Mandevilla Mandoni* Rusby. Sorata, Bolivia, Apr. 19, 1920, 556.

While somewhat like *Puccinia obliqua* Berk. & Curt., which occurs on members of the Asclepiadaceae, this micro-form seems sufficiently distinct morphologically, and occurs on a different host family. The septum is only rarely oblique.

It is especially interesting to note that the teliospores germinate with a two celled basidium. Elsewhere (Mem. Torrey Club 18: 22-27. 1931) I have reviewed the available knowledge with reference to the occurrence of two celled basidia in micro- and endo-forms, and have discussed the probable significance of this phenomenon. The two celled basidium provides an easily determined external indication of a simplified nuclear history. Spe-

cies in which the spores germinate in this way should be well worth investigating cytologically.

229. *Uredo Condylarci* Jackson & Holway, sp. nov.

II. Uredinia hypophyllous, scattered or somewhat gregarious, small, round, 0.2–0.3 mm. across, cinnamon brown, early naked, pulverulent, ruptured epidermis not conspicuous; paraphyses abundant, peripheral, at first incurved, becoming somewhat erect, 60–225  $\mu$  in length, 6  $\mu$  wide at apex, up to 12  $\mu$  at base, wall thin, colorless or light golden brown, 1–1.5  $\mu$ , sometimes thickened to 4  $\mu$  on outer side at base; urediniospores ellipsoid, obovate or pyriform, 19–25 by 32–38  $\mu$ ; wall thin, 1–1.5  $\mu$ , light cinnamon brown, closely and minutely echinulate, the pores obscure.

*Condylarpon Rauwolfiae* Muell. Arg. São João, São Paulo, Brazil, July 2, 1922, 1986.

The very long erect paraphyses make this a well marked species. It is possible that it may be the same as *Uredo Apocynaceae* P. Henn., which was described from Brazil on an unknown member of the Apocynaceae. Authentic material has not been available. In that species the paraphyses are described as being only 35–65  $\mu$  long.

SPECIES ON ASCLEPIADACEAE

230. PUCCINIA ARAUJAE Lév. Ann. Sci. Nat. III. 5: 69. 1845.

*Puccinia Schnyderi* Speg. Anal. Soc. Cient. Arg. 10: 8. 1880.

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*Arauja sericifera* Brot. Pinheiros, São Paulo, Brazil, March 9, 1922, 1620.

A short cycle form apparently sufficiently distinct to justify recognition. The spores are more elongated than in *P. obliqua*.

231. PUCCINIA CONCRESCENS Ellis & Ev.; Arth. Mycologia 7: 240. 1915.

*Puccinia compacta* Kunze in Sydow, Monog. Ured. 1: 334. 1902 (not Berk. 1855).

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*Asclepias curassavica* L. Juiz de Fora, Minas Geraes, Brazil, Dec. 14, 1921, 1402.

The above name seems to be the most acceptable one for this

distinct micro-form. The only other record of its occurrence from South America is from Surinam. It is known also from Porto Rico, Cuba and the Bahamas in the West Indies.

232. UROMYCES ASCLEPIADIS Cooke, Grevillea 5: 152. 1877.

*Uredo Asclepiadis* Schw.; Berk. & Curt. Jour. Acad. Sci. Phila. II, 2: 282. 1853.

*Trichobasis Howei* Peck, Ann. Rep. N. Y. State Mus. 23: 58. 1873.

*Uromyces Howei* Peck, Ann. Rep. N. Y. State Mus. 30: 75. 1879.

*Uredo asclepiadina* Speg. Anal. Mus. Nac. Buenos Aires III. 12: 316. 1909.

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*Asclepias curassavica* L. Lima, Peru, July 21, 1920, 776; Rio de Janeiro, Brazil, Aug. 13, 1921, 1035, Nov. 14, 1921, 1301; Cascadura, Rio de Janeiro, Brazil, Aug. 24, 1921, 1068; Sabara, Minas Geraes, Brazil, Dec. 2, 1921, 1362; Juiz de Fora, Minas Geraes, Brazil, Dec. 17, 1921, 1403.

A common species in North and South America and the West Indies. While in North America the species is known on a considerable number of species of *Asclepias*, most, if not all, of the South American collections are on the host listed above.

233. PUCCINIA OBLIQUA Berk. & Curt.; Berk. Jour. Linn. Soc. 10: 356. 1869.

*Puccinia Gonolobi* Rav.; Berk. Grevillea 3: 54. 1874.

*Puccinia Cynanchi* Lagerh. Bol. Soc. Brot. 7: 129. 1889.

*Puccinia Kunzeana* P. Henn. Hedwigia 33: 230. 1894.

*Puccinia Philibertiae* Ellis & Ev. Bull. Torrey Club 22: 60. 1895.

*Puccinia Oxypetali* P. Henn. Hedwigia Beibl. 38: 129. 1899.

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*Oxystelma* sp. Sorata, Bolivia, May 3, 1920, 588.

*Philibertia* sp. Sorata, Bolivia, Apr. 15, 1920, 525.

*Unidentified* asclepiad vine. Reserva Florestal, Itatiaya, Brazil, May 9, 1922, 1831; Bosque da Saude, São Paulo, Brazil, March 22, 1922, 1668.

This characteristic micro-form is common throughout South and Central America as well as the Southern United States and the West Indies. It is probable that there are other synonyms which belong here among the numerous species of *Puccinia* described on members of this host family from South America.

#### SPECIES ON CONVOLVULACEAE

234. COLEOSPORIUM IPOMOEAE (Schw.) Burrill, Bull. Ill. Lab. Nat. Hist. **2**: 217. 1885.

*Uredo Ipomoeae* Schw. Schr. Nat. Ges. Leipzig **1**: 70. 1822.  
*Coleosporium guaranticum* Speg. Anal. Soc. Ci. Argent. **17**: 95.  
1884.

*Uredo Ipomoeae-pentaphyllae* P. Henn. Hedwigia **35**: 252.  
1896.

*Peridermium Ipomoeae* Hedg. & Hunt, Mycologia **9**: 239.  
1917.

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*Ipomoea acuminata* R. & S. Cascadura, Rio de Janeiro,  
Brazil, Jan. 12, 1922, 1471.

*Ipomoea purpurea* Lam. Santa Clara, above Lima, Peru,  
July 23, 1920, 784.

*Ipomoea* sp. Paineiras, Rio de Janeiro, Brazil, Aug. 17,  
1921, 1044; Friburgo, Rio de Janeiro, Brazil, Jan. 7, 1922,  
1466.

*Operculina glabra* (Aubl.) Chois. Hacienda "La Florida,"  
Sur Yungas, Bolivia, May 28, 1920, 671; Pocos da Caldas,  
São Paulo, Brazil, Apr. 10, 1922, 1723.

235. PUCCINIA CONVOLVULI (Pers.) Cast. Obs. **1**: 16. 1842.

*Uredo Betae Convoluti* Pers. Syn. Fung. **221**. 1801.

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*Convolvulus* sp. Therezopolis, Rio de Janeiro, Brazil, Oct. 6,  
1921, 1198.

This appears to be the first record of this rust in South America. There can be no doubt of the identification as a few typical teliospores were found, though the collection is mostly of uredinia.

236. PUCCINIA CRASSIPES Berk. & Curt.; Berk. Grevillea **3**: 54.  
1874.

*Puccinia Ipomoeae* Cooke; Lagerh. Tromso Müs. Aarsh. **17**:  
61. 1895.

*Puccinia Ipomoeae-panduratae* Sydow, Monog. Ured. **1**: 323.  
1902.

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*Ipomoea polymorpha* Riedel, Arthur. Anvim, São Paulo,  
Brazil, March 15, 1922, 1636.

*Ipomoea*. Therezopolis, Rio de Janeiro, Brazil, Sept. 29,  
1921, 1170.

This characteristic -opsis form has been reported previously from South America from Argentina, Ecuador, Brazil and Colombia, usually under one or the other of the synonyms. It is a common form in Central America and the West Indies and in the Southern United States.

237. PUCCINIA DICHONDRAE Mont. in Gay, Fl. Chil. **8**: 46.  
1852.

*Puccinia Dichondrae* Berk. Jour. Linn. Soc. **13**: 173. 1872.

*Puccinia Berkeleyana* DeToni in Sacc. Syll. Fung. **7**: 717.  
1888.

*Puccinia munita* F. Ludwig, Zeits. Pflanzenkr. **2**: 133. 1892.

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*Dichondra* sp. Constitucion, Chile, Oct. 18, 1919, 129;  
Concepcion, Chile, Oct. 29, 1919, 145; Los Angeles, Chile,  
Oct. 30, 1919, 151; Cochabamba, Bolivia, March 12, 1920,  
404; La Paz, Bolivia, March 20, 1920, 441; Sorata, Bo-  
livia, Apr. 16, 1920, 528, Apr. 27, 1920, 578.

An *Aecidium* has been described by Neger and Hariot on *Dichondra*, which is assigned to this species by Sydow (Monog. Ured. **2**: 321. 1902). We have excluded the aecial names from the synonymy on the ground that this species is quite certainly a micro-form. The aecidium may be interpreted as the aecial stage of a correlated heteroecious rust or, since it is apparently systemic, it may prove to be an *Endophyllum*. Another possibility exists, however, which may be the true situation. I have in another publication (Mem. Torrey Club **18**: 58-64. 1931) discussed transitional -opsis forms and their probable relation to correlated micro-forms on the one hand and to heter-eu-forms

on the other. It is possible that there exists a form with an -opsis life history correlated with the micro-form *P. Dichondrae* and representing a transitional condition which has developed in the formation of the micro-form from the parent heter-eu-form.

238. ***Puccinia distinguenda* (Sydow) Jackson & Holway, comb. nov.**

*Aecidium distinguendum* Sydow, Monog. Ured. 4: 131. 1923.

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*Ipomoea fistulosa* Mart. Guayaquil, Ecuador, July 30, 1920, 794 (type).

The collection listed above bears abundant telia as well as aecia. The aecia agree perfectly with Sydow's description of *Aecidium distinguendum*. The telia are primarily epiphyllous, associated with the aecial clusters or on the same spots, and evidently from the same mycelium, small, round, early naked, jet black, pulverulent, ruptured epidermis at first noticeable. The teliospores are ellipsoid or oblong, 28–32 by 42–56  $\mu$ , rounded or sometimes obtuse above, rounded below, not constricted at the septum. The wall is dark chestnut brown, 3.5–4  $\mu$  thick, slightly thickened 5–6  $\mu$  at the apex and at the angles formed by the septum, evenly and finely verrucose. The pedicel is once to twice the length of the spore, colorless or slightly tinted next the spore, 10–11  $\mu$  at point of attachment, soon collapsing.

While the aecia somewhat resemble those of *Puccinia nocticolor* Holway, the teliospores are quite different. Pycnia were not observed with the aecia.

239. ***Puccinia Lithospermi* Ellis & Kellerm. Jour. Myc. 1: 2. 1885.**
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*Evolvulus sericeus* Sw. Cochabamba, Bolivia, March 2, 1920, 360.

The above collection agrees with North American collections of this species. Arthur (N. Am. Fl. 7: 791. 1926) has reduced this name to synonymy and considers it the same as *Puccinia tuyatensis* Speg. The latter species, however, is described as

having the teliospore wall of uniform thickness. There is no evidence in the Arthur herbarium that the type of *P. tuyatensis* has been examined. On this account it seems best to record the species as above.

Spegazzini describes another species, *P. enecta* Speg. on this host genus, which may be the same as the above.

240. PUCCINIA OPULENTA Speg. Anal. Soc. Ci. Argent. **9**: 170.  
1880.

*Aecidium Ipomoeae* Speg. Anal. Soc. Ci. Argent. **9**: 173. 1880.  
*Allodus opulenta* Orton, Mem. N. Y. Bot. Garden **6**: 195. 1916.

*Ipomoea* sp. Petropolis, Rio de Janeiro, Brazil, Oct. 18, 1921, *1226*; Raiz da Serra, Rio de Janeiro, Brazil, Nov. 6, 1921, *1283*; Bello Horizonte, Minas Geraes, Brazil, Nov. 30, 1921, *1349*; Barbacena, Minas Geraes, Brazil, Dec. 12, 1921, *1387*; Nova Friburgo, Rio de Janeiro, Brazil, Jan. 1, 1922, *1436*; São Paulo, Brazil, Jan. 20, 1922, *1481*; Juquery, São Paulo, Feb. 14, 1922, *1556*; Tremembé, São Paulo, Brazil, March 6, 1922, *1616*; Pocos da Caldas, São Paulo, Brazil, Apr. 8, 1922, *1714*; Reserva Florestal, São Paulo, Brazil, May 9, 1922, *1826*, *1830*, May 14, 1922, *1851*.

Evidently a common species in Brazil and Argentina. It has also been reported from Ecuador and from St. Thomas in the West Indies.

241. UROMYCES GEMMATUS Berk. & Curt.; Berk. Jour. Linn. Soc. **10**: 357. 1869.

*Uredo spinulosa* Dietel, Hedwigia **36**: 36. 1897 (not Sacc. 1891).

*Uredo Dieteliana* Sacc. & Sydow in Sacc. Syll. Fung. **14**: 395. 1899.

?*Uromyces giganteus* Dietel, Hedwigia **36**: 26. 1897 (not Speg. 1879).

?*Uromyces brasiliensis* Trotter, Ann. Myc. **2**: 533. 1904.

*Jacquemontia ferruginea* Choisy. Bosque da Saude, São Paulo, Brazil, Jan. 29, 1922, *1509*; São Caetano, São Paulo, Brazil, March 8, 1922, *1617*.

*Jacquemontia punctantha* Don. Guayaquil, Ecuador, July 31, 1920, 799.

*Jacquemontia* sp. Bello Horizonte, Minas Geraes, Brazil, Nov. 27, 1921, 1346; Campos do Jordão, São Paulo, Brazil, Apr. 28, 1922, 1786; Reserva Florestal, Itatiaya, Brazil, May 7, 1922, 1823; Guaruja, Santos, Brazil, July 18, 1922, 2015.

We have included here all the collections having thick walled spiny urediniospores and teliospores with greatly thickened apices. Some of our collections fit the species as described by Arthur in the North American Flora. Others, however, have much larger teliospores and fit the description and measurements of *U. brasiliensis*. The latter (as *U. giganteus*) was described with telia only, but has not been reported elsewhere than at the type locality. It would seem that this is a variable species and that the more northern collections have smaller teliospores than most of those from South America. Sydow found teliospores in the type collection of *Uredo spinulosa* which appear to fit our material well.

242. *Uromyces vicinus* Jackson & Holway, sp. nov.

II. Uredinia amphigenous, chiefly hypophyllous, scattered or gregarious in small groups, small, round, 0.2–0.4 mm. across, early naked, cinnamon brown, pulverulent, ruptured epidermis noticeable; urediniospores ellipsoid or obovoid, 19–22 by 24–28  $\mu$ ; wall thin, 1  $\mu$  or less, colorless or slightly tinted golden brown, closely and finely echinulate; pores obscure, 2 or 3, approximately equatorial.

III. Telia like the uredinia, blackish brown, compact; teliospores somewhat variable, ellipsoid, obovoid or oblong, 18–23 by 28–37  $\mu$ , rounded or obtuse above, rounded or often somewhat narrowed below; wall chestnut brown, thin, 1  $\mu$  or less, greatly thickened at apex, 6–12  $\mu$ , often somewhat lamellate, smooth; pedicel colorless or slightly tinted next the spore, short, deciduous.

*Ipomoea* sp. Petropolis, Rio de Janeiro, Brazil, Oct. 30, 1921, 1255; Barbacena, Minas Geraes, Brazil, Dec. 12, 1921, 1388; São João, São Paulo, Brazil, March 19, 1922, 1656, July 2, 1922, 1995; Tremembe, São Paulo, May 30, 1922, 1905; Juquery, São Paulo, June 12, 1922, 1961 (type); Alto da Serra, São Paulo, Brazil, June 14, 1922, 1964.

A characteristic species which differs from the preceding in both uredinial and telial characters.

#### SPECIES ON BORAGINACEAE

243. AECIDIUM BRASILIENSE Dietel, Hedwigia **36**: 35. 1897.

*Cordia discolor* Cham. Rio de Janeiro, Brazil, Nov. 13, 1921, 1297.

*Cordia obscura* Cham. Therezopolis, Rio de Janeiro, Brazil Oct. 2, 1921, 1185.

*Cordia* sp. San Francisco, Nictheroy, Rio de Janeiro, Brazil, Sept. 23, 1921, 1147.

A common species in southern Brazil. The report by Arthu, of this species from Trinidad is an error, as shown by an examination by the writer of all the specimens. They are *Aecidium Cordiae* P. Henn. The collection reported by Hennings from Yuremaguas, Peru (Ule 3242), was made the type of a new species *Aec. Lindavianum* Syd.

244. AECIDIUM CORDIAE P. Henn. in Engl. Bot. Jahrb. **17**: 491. 1893.

*Cordia curassavica* R. & S. Freguesia, Rio de Janeiro, Brazil, Nov. 18, 1921, 1318; Bello Horizonte, Minas Geraes, Brazil, Nov. 21, 1921, 1323.

*Cordia urticaeifolia* Cham. Friburgo, Rio de Janeiro, Brazil, Jan. 6, 1922, 1463.

A characteristic species easily distinguished from the preceding by the thickened apices of the aeciospores. The type locality is usually given as Santo Domingo, but this is now considered an error for Haiti. The species is also known from Trinidad and at least two previous collections have been made in Brazil. Arthur (N. Am. Fl. 7: 635. 1924) lists *Aecidium brasiliense* Diet. as a synonym, but this is clearly an error.

245. AECIDIUM TOURNEFORTIAE P. Henn. Hedwigia **34**: 338. 1895.

*Tournefortia brachiata* DC. Juiz de Fora, Minas Geraes, Brazil, Dec. 17, 1921, 1404; Friburgo, Rio de Janeiro, Brazil, Jan. 2, 1922, 1445.

*Tournefortia grandifolia* Fresen. Bello Horizonte, Minas Geraes, Brazil, Dec. 4, 1921, 1364.

*Tournefortia* sp. São Paulo, Brazil, Jan. 22, 1922, 1489.

This species is common in southern Brazil and has also been reported from Porto Rico, Cuba and Panama.

246. ALVEOLARIA CORDIAE Lagerh. Ber. Deuts. Bot. Ges. 9: 346. 1891.

*Cordia cylindrostachya* R. & S. El Chaco, Prov. Sur Yungas, Bolivia, May 24, 1920, 642.

*Cordia* sp. El Chaco, Prov. Sur Yungas, Bolivia, May 24, 1920, 640.

Reported originally from Ecuador this interesting species is now known also from Colombia, Panama, Costa Rica, Guatemala, and from Jamaica.

247. *Puccinia Tournefortiae* Jackson & Holway, sp. nov.

0. Pycnia epiphyllous, closely aggregated in small groups of 3 to 8 on yellowish spots, noticeable, punctiform, dark reddish brown, globoid or depressed globoid, deep seated, 100 to 125  $\mu$  in breadth and height, ostiolar filaments short, not conspicuous.

III. Telia hypophyllous, usually forming a circular group 1-2 mm. across, with the pycnia in the centre on the opposite side of the leaf, confluent, early naked, compact, becoming pulvinate, golden brown, ruptured epidermis at first noticeable; teliospores elongate clavate or cylindrical, 22-29 by 56-100  $\mu$ , rounded or obtuse above, narrowed to pedicel below, not or slightly constricted, wall colorless or tinted golden brown, thin, 1  $\mu$  at sides, gradually thickened at apex, 6-12  $\mu$ , greatly thickened also at angles of lower cell just beneath the septum, smooth; upper cell usually broader and shorter than lower cell; pedicel short, colorless.

*Tournefortia fuliginosa* H.B.K. Sorata, Bolivia, May 4, 1920, 589.

This species appears to be somewhat like *P. tournefortiicola* Speg. In that species, however, the spores are considerably smaller. The teliospores in the above species germinate at once with a four celled promycelium. Three celled spores are not uncommon.

248. *Uredo Tournefortiae* Jackson & Holway, sp. nov.

II. Uredinia hypophyllous, scattered, small, round, 0.2–0.4 mm. across, early naked, pulverulent, light cinnamon brown, ruptured epidermis noticeable; urediniospores globoid or ellipsoid, 16–19 by 19–21  $\mu$ ; wall colorless or nearly so, 1–1.5  $\mu$ , closely and finely echinulate, the pores obscure.

*Tournefortia suaveolens* H.B.K. Huigra, Prov. Chimborazo, Ecuador, Aug. 3, 1920, 818.

Quite distinct from any *Uredo* previously reported on this host family. No pycnia or teliospores could be found.

249. *UROMYCES DOLICHOSPORUS* Diet. & Holw.; Holway, Bot. Gaz. 31: 327. 1901.

*Uredo pachystegia* Diet. Hedwigia 38: 257. 1899.

*Uromyces Tournefortiae* P. Henn. Hedwigia 47: 267. 1908.

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*Tournefortia psilostachya* H.B.K. Huigra, Prov. Chimborazo, Ecuador, Aug. 3, 1920, 813.

*Tournefortia sericea* Vahl. Juiz de Fora, Minas Geraes, Brazil, Dec. 18, 1921, 1412; Therezopolis, Rio de Janeiro, Brazil, Oct. 2, 1921, 1183; Friburgo, Rio de Janeiro, Brazil, Jan. 2, 1922, 1446.

*Tournefortia* sp. Reserva Florestal, Itatiaya, Brazil, May 10, 1922, 1841; Santa Anna, São Paulo, Brazil, May 25, 1922, 1881, 1882; Taipas, São Paulo, Brazil, June 10, 1922, 1950.

The type locality for this brachy-form is in Oaxaca, Mexico. This species is not infrequent in southern Mexico and is also known from Cuba and Porto Rico. It has not been collected frequently in South America. I find only the reference of the type collection of *U. Tournefortiae* which was made at Rio de Janeiro (Ule 2535) and the specimen on which *Uredo pachystegia* Diet. was based. The latter was reported as on *Vernonia* but according to Sydow (Monog. Ured. 4: 568. 1924) the host is *Tournefortia*.

250. TRICHOPSORA TOURNEFORTIAE Lagerh. Ber. Deutsch. Bot. Ges. 9: 347. 1891.

*Tournefortia* sp. Huigra, Prov. Chimborazo, Ecuador, Aug. 4, 1920, 834; Quito, Ecuador, Aug. 14, 1920, 892; Cuenca, Ecuador, Sept. 10, 1920, 967.

This remarkable micro-form is known only from Ecuador. The long hair-like columns of teliospores evidently adhere through the gelatinization of the spore wall. No evidence of a peridium has been noted. While no detailed study of the development of the sori has been made, it is quite evident that the spores are formed in chains. A careful study of crushed mounts of spore columns stained with cotton blue in lactophenol reveals the presence among the spores of additional, narrow, elongated binucleate cells, also with gelatinous cell walls. These are the "sterilen Zellen" of Lagerheim (l.c.). These narrow cells, which are about one fourth the diameter of the spores, appear to be connected with them by greatly elongated extensions of the gelatinous spore wall. Their presence may be demonstrated even after the spores have germinated, by the deeply stained contents. It seems reasonable to interpret these elongated cells as intercalary cells.

The spores germinate by the development of internal transverse walls which divide the spore into four cells. Rather stout sterigmata develop from each cell. These are short in the spores which occur on the outsides of the spore column, but are much longer from the internal spores. The basidiospore is obovate 11-13 by 17.5-18.5  $\mu$ .

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